cera glabra was investigated by Milanez (1937); Record and Garratt (1925) and Desch (1948) described the secondary xylem anatomy of *Phyllostylon brasiliensis*. Record and Mell (1924) and Record and Hess (1943) described some features of the wood anatomy of several genera, including *Ampelocera, Celtis, Chaetoptelea, Phyllostylon, Planera, Trema, Ulmus*. In a work entitled "Phylogénie des Ulmacées," Houlbert (1899) discussed the need of using "echantillons d'age avancé" in phylogenetic studies based on wood anatomy He studied a complete range of *Ulmus* woods of various ages and attempted to correlate yearly differences in *Ulmus* with mature wood characters of related genera to show evolutionary development. Major summary works dealing with secondary xylem anatomy and general anatomy of some genera of Ulmaceae include those of DeBary (1884), Solereder (1908), and of Metcalfe and Chalk (1950).

Works pertaining to aspects of anatomy other than wood structure vary in their completeness. A study of the leaf anatomy of 14 genera and 80 species of the Ulmaceae was carried out by Priemer (1893). Leaf ontogeny of *Zelkova serrata* was investigated by Soma (1965). Gardiner (1965) attempted to correlate leaf anatomy and geographic distribution in *Trema*. Petiolar anatomy of *Celtis* and several other urticalean genera was studied by Sarabhai and Saxena (1961).

Bechtel (1921) published work on the floral anatomy of the Urticales, including Ulmaceae (five species of *Ulmus*, one species of *Celtis*). Several studies have been made of megasporogenesis, microsporogenesis, and embryology; for example that of Shattuck (1905) on *Ulmus americana*; of Capoor (1937) on *Holoptelea integrifolia*; of Eckardt (1937) on *Ulmus montana, Celtis tournefortii* and genera of related pseudomonomerous families; and of R. I. Walker (1938, 1949) on various species of *Ulmus*. General summary works dealing with embryology which include some genera of the Ulmaceae are listed in the work of Maheshwari (1950), of Eames (1961), and of Davis (1966). The embryo sac of *Celtis* is of the Polygonum type and that of *Ulmus* of the Adoxa or Drusa type.

The secondary phloem anatomy of *Ulmus, Celtis, Gironniera, Trema,* and *Zelkova* was investigated by Zahur (1959). Sieve tube ontogeny in *Ulmus americana* has been investigated with the light microscope (Evert *et al.*, 1969) and with the electron microscope (Evert & Deshpande, 1969).

SECRETIONS AND CHEMOTAXONOMY

Various intracellular substances, such as silica, calcium carbonate, and mucilage, have been reported to occur in different organs, tissues, and cells of most ulmaceous genera. Amos (1952) reported the presence of vitreous silica in vessels and parenchyma cells of the secondary xylem of *Gironniera*. He also stated that wood specimens of *Aphananthe, Celtis, Holoptelea, Phyllostylon, Trema, Ulmus,* and *Zelkova* showed no evidence of silica formation. Priemer (1893) reported that the leaf epidermis and hairs of the species of *Zelkova, Aphananthe, Ulmus, Celtis,* and *Trema* he investigated were silicified. Various techniques for analysis of silica are contained in Satake (1931), Uber (1940), Amos (1952), Lanning, *et al.* (1958), and Jones and Handreck (1967). A recent review of silicon physiology can be found in Lewin and Reimann (1969). Actual chemical analyses for the presence of silica were beyond the scope of this investigation.

The presence of calcium carbonate in old vessels of wood was reported in Haberlandt (1928) for *Ulmus glabra* and *Celtis orientalis*. Secondary xylem deposits of calcium carbonate were noted in several species of *Ulmus*, *Celtis*, and *Phyllostylon* by Record (1927). Priemer (1893) reported the presence of calcium carbonate in the form of cystoliths in the leaves of several ulmaceous genera. Satake (1931) found calcium carbonate cystoliths in *Celtis* and *Trema* leaves. Pireyre (1961) discussed cystoliths from morphologic, histologic, and physiologic bases in two species of *Celtis* as well as other non-ulmaceous genera. Metcalfe and Chalk (1950) listed various genera reported to have calcium carbonate deposits. Techniques for the determination of calcium carbonate can be found in Satake (1931), Scott (1946), and Pireyre (1961). Chemical analyses of calcium carbonate were beyond the scope of this study.

Mucilage has been identified in the past by its viscous appearance in sectioned tissues, the chemical nature of this substance has been little investigated and the microscopist has had to rely on nonspecific visual observations rather than specific histochemical tests. The literature is replete with reports on mucilaginous and gummy materials in the leaves, bark, and roots of several ulmaceous genera and species, especially *Ulmus rubra* and *U. glabra* bark which has a high mucilage content, Lawrence (1951), Metcalfe and Chalk (1950), and Hutchinson (1969).

Smith and Montgomery (1959) discussed plant gum and mucilage chemistry. Practical histochemical implications of their work are yet to be realized, but because of the apparent ubiquitous occurrence of these or related substances in Ulmaceae, a brief consideration of gum and mucilage chemistry is perhaps in order at this point. Mucilages are products of normal plant metabolism and may serve as food reserves. There is no clear chemical distinction between gums and mucilages and both are complex polysaccharides. The complexity of these compounds is due to the type of linkage and component building units; mucilage bodies result from regularly spaced side chains, whereas gums have irregular substitutions. Mucilages give rise to thick gels; gums dissolve in water and give clear solutions with adhesive properties. TABLE 3 shows Smith and Montgomery's conceptual classification of gums and mucilages. The hydrolysis products of *Ulmus rubra* (as *U. fulva*) mucilage are D-galactose, 3-0-methyl-D-galactose, L-rhamnose, and D-galacturonic acid (Robinson, 1963).

In the only comparative chemotaxonomic study encountered, Lebreton (1965) discussed the relationships within the Urticales based on flavonoids. He specifically analyzed species of *Celtis* and *Ulmus* and his results are noted in the DISCUSSION.

TABLE 3. **Classification of gums and mucilages**[a]

GROUP I		GROUP II
Acidic gums and mucilages containing:		Neutral gums and mucilages containing:
Acid components	*Neutral components*	
L-guluronic acid	Hexoses	Hexoses
D-glucuronic acid	Pentoses	6-Deoxyhexoses
D-galacturonic acid	6-Deoxyhexoses	Pentoses
Sulfate groups	Sugar alcohols	Sugar alcohols
Phosphate groups	Ethers of all of the above	Ethers of all of the above
Ethers of all of the above		

[a] From Smith & Montgomery (1959).

PROBLEMS AND OBJECTIVES

A study of the wood and leaf anatomy should provide additional information for phylogenetic studies of Ulmaceae and at the same time help to clarify ordinal relationships and intrafamilial systematic problems. The latter include the taxonomic status of the two major subdivisions of Ulmaceae and of the genera *Chaetoptelea, Mirandaceltis*, and *Gironniera*. Anatomical data will be correlated with other pertinent information to provide a firmer basis for an interpretive discussion of the affinities and composition of Ulmaceae.

In addition, leaf and wood anatomy can be used in the identification of species from local floras, which might be useful in the identification of commercially important ulmaceous timbers, possible drug plants, and potential ornamentals. A knowledge of wood anatomy is imperative in some aspects of forensic botany. *Ulmus* species and varieties vary in their susceptibility to Dutch elm disease and elm phloem necrosis. These are, at least in part, diseases of the vascular system, and susceptibility and resistance may be related partially to differences in the vascular tissue, which a thorough anatomical study might reveal, making possible a more effective breeding program for disease resistance.

MATERIALS AND METHODS

For the most part, the terminology of xylem anatomy used here is in agreement with that suggested by the Committee on Nomenclature of the International Association of Wood Anatomists (1957). Terms used to describe overall venation patterns in leaves are taken from von Ettingshausen (1861). Additional terms conform to current usage and deviation from such usage is explained where employed in the text.

Standard techniques were used in preparing specimens for observation. Dried wood specimens were hydrated in boiling water, dehydrated in ethyl alcohol, and embedded in celloidin. Wood specimens preserved in formalin-acetic acid-alcohol (FAA) were dehydrated and embedded in celloidin. Transverse, radial, and tangential sections were cut on a sliding microtome, stained with Heidenhain's iron-alum haematoxylin, and counterstained with safranin. Wood macerations were prepared using Jeffrey's fluid, washed in water, stained with safranin, and dehydrated with tertiary-butyl alcohol. Sections and macerations were mounted in Canada balsam.

Leaves preserved in FAA and dried leaves from herbarium specimens were used in this study. All dried leaves were first hydrated in boiling water; clearings of leaves were made following Arnott's (1959) technique using 5 percent sodium hydroxide, followed by a water wash, and treatment with a saturated aqueous solution of chloral hydrate. Leaves were then washed with water, stained with aqueous safranin, dehydrated in ethyl alcohol, and mounted in Canada balsam. Transverse and paradermal sections of leaves were embedded in paraffin and cut on a rotary microtome. Sectioned leaves were stained with safranin and fast green, cleared in clove oil and toluene, and mounted in Canada balsam.

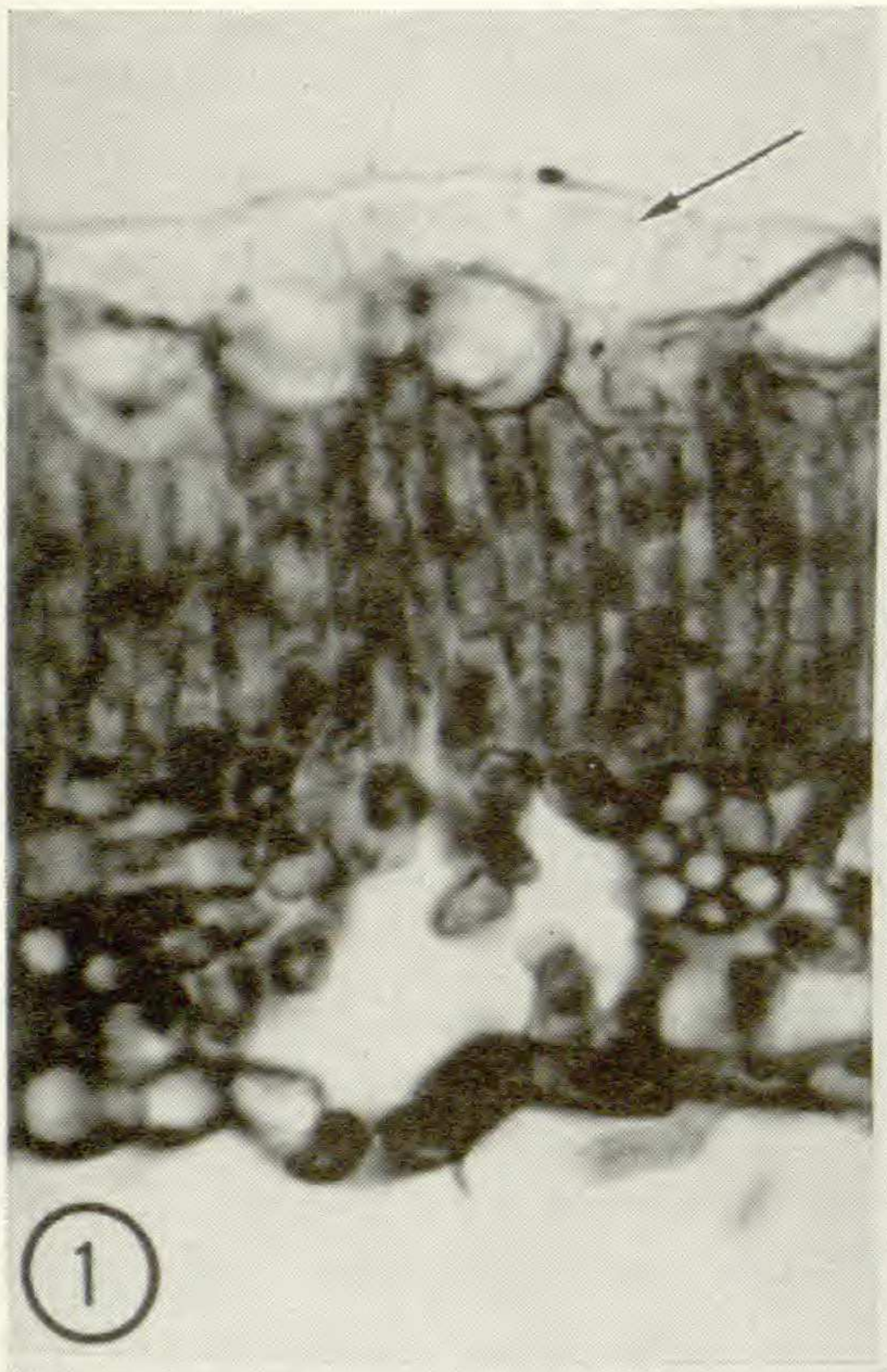
Pore distributions expressed as percentages were obtained by counting 10 microscope fields from the transverse sections. Tangential pore diameters, vessel element lengths, and imperforate tracheary element lengths are based on 50 measurements each. Tangential pore diameters were measured only in the last completely formed growth ring. For all ring porous specimens, 25 tangential pore diameters were measured from the first formed portion of the growth ring and 25 from the last formed portion of the growth ring. Vessel elements were measured from tip to tip to obtain the length. From the leaf clearings the approximate frequency of cystoliths was obtained by counting the cystoliths contained in a one millimeter square area of leaf surface.

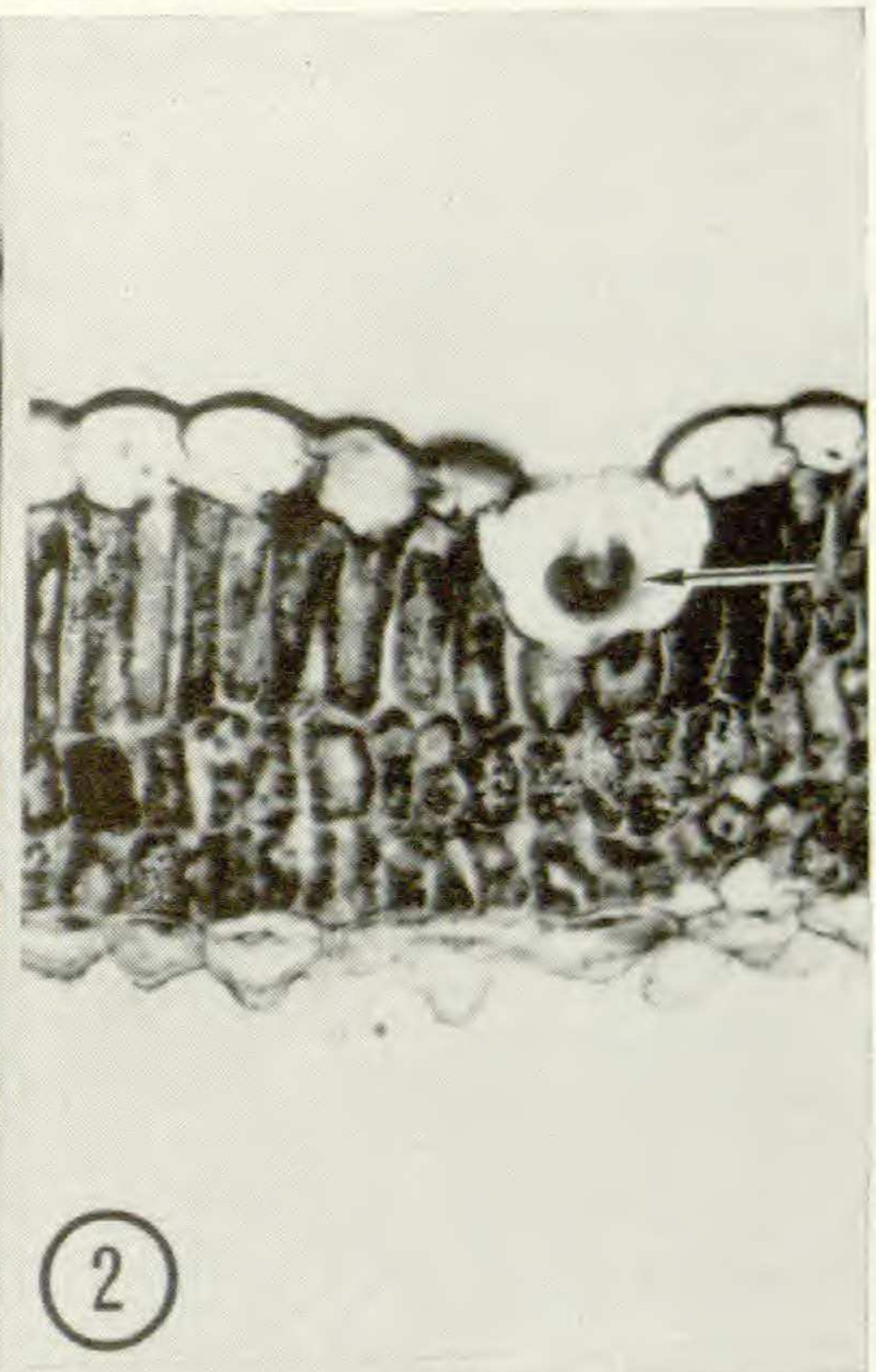
About 25 percent of the microscope slides of wood specimens employed in this study were prepared in the laboratory of Dr. Oswald Tippo. Preparation of these specimens was probably the same as employed here except for softening in hydrofluoric acid for the hardest specimens. Lists of all specimens used in this study are given in TABLES 4a, 4b, and 4c. Identifications used are those originally accompanying specimens, except that nomenclature of cultivated species follows Rehder (1940) and that of species indigenous to the United States follows Little (1953).

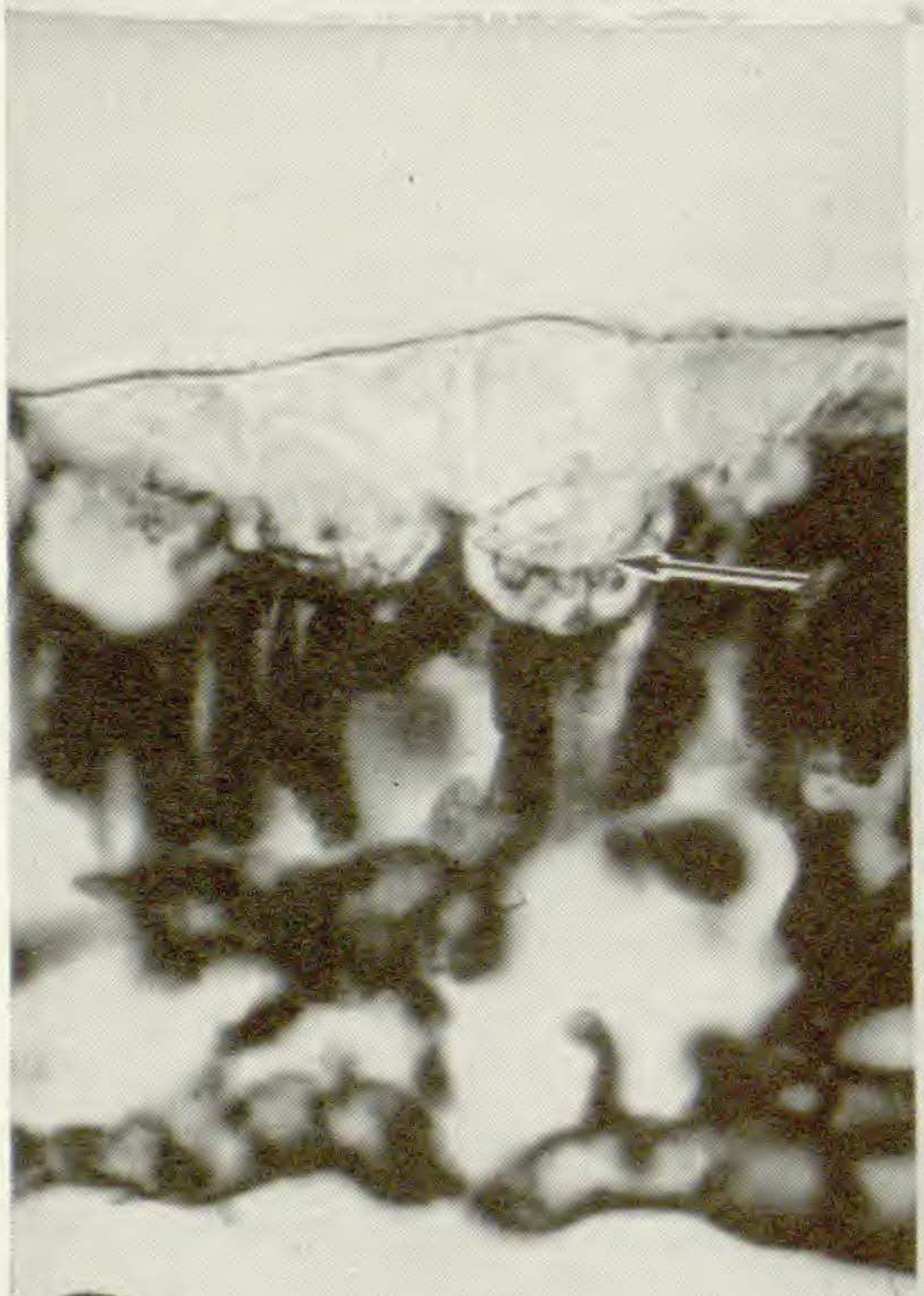
Microchemical tests were not performed to determine the presence of silica, mucilage, or calcium carbonate, each of which has been reported previously in cells and tissues of Ulmaceae. When these terms are used they are in general agreement with reports from the literature; silica has a glass-like appearance, mucilage is viscous to frothy in texture, and calcium carbonate stains to varying degrees with safranin and fast green. (For TABLES 4a, 4b, and 4c, see pages 574–584.)

RESULTS

The sequence of genera for the anatomical descriptions of leaf and wood







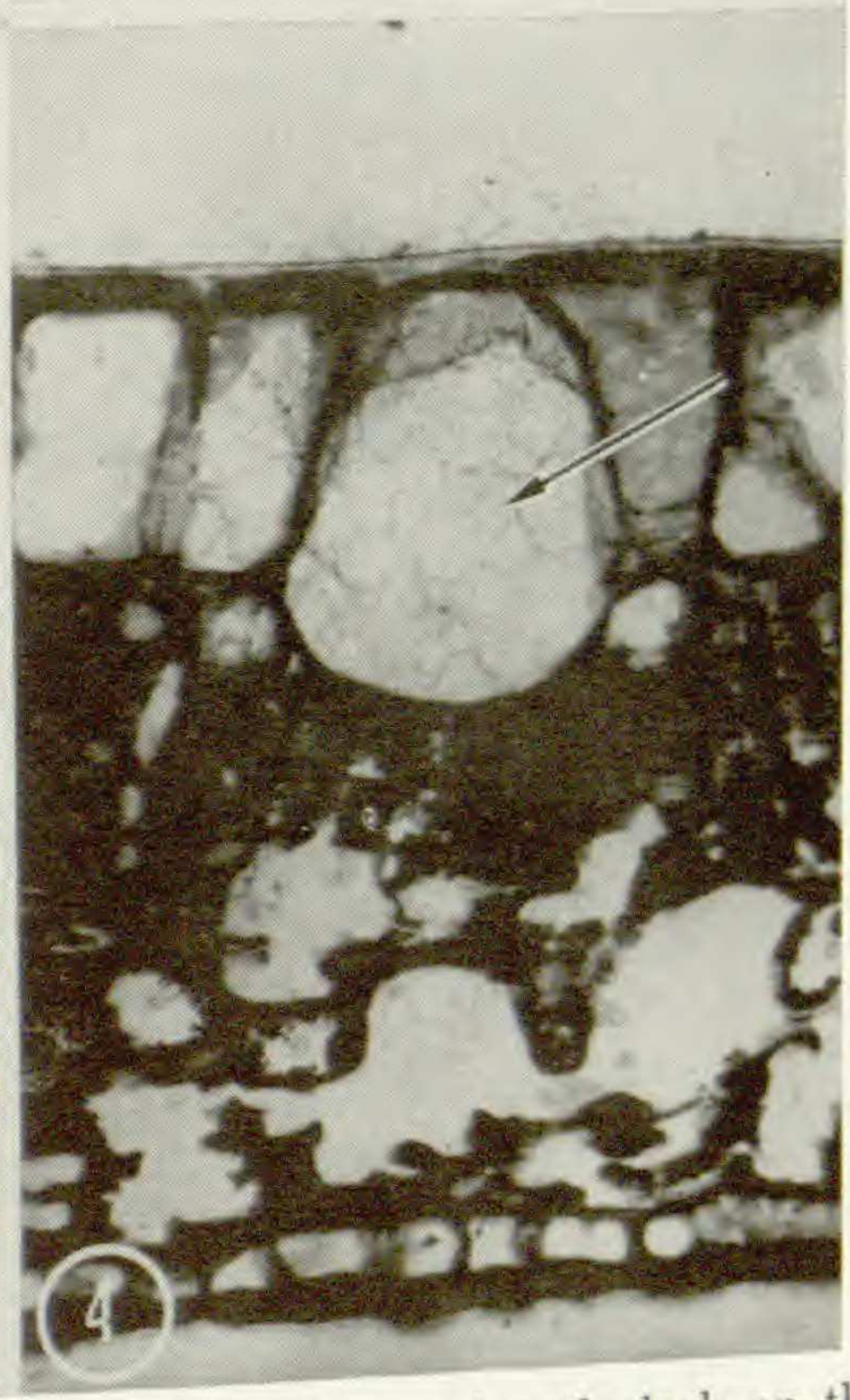


FIGURE 1, *Zelkova sinica*. Cross section of leaf with a mineral plack on the upper epidermis, × 320. 2, *Celtis tournefortii*. Cross section of leaf with a cystolith in the upper epidermis and a compact spongy mesophyll, × 320. 3, *Ulmus parvifolia*. Cross section of leaf with a pegless cystolith in an upper epidermal cell below a mineral plack, × 320. 4, *Chaetachme microcarpa*. Cross section of leaf with an enlarged upper epidermal cell containing frothy mucilage, × 320.

follows Hutchinson (1967), except for *Chaetoptelea* which he included in *Ulmus*.

In the generic descriptions which follow, the number of species, in parentheses, is followed by the number of specimens if there were more specimens than species examined.

LEAF

Since several descriptive terms refer to structures and substances which are not widespread, their usage in this paper is explained here. Silica or siliceous refers to any material which is glass-like in appearance; the term mineral plack refers to the silica and/or calcium carbonate covering an epidermal area composed of several cells, i.e., both on the surface and between the cells (FIGURE 1).

Cystolith refers to an anisotropic crystalline concretion of both calcium carbonate and silica (Pireyre, 1961) of varying shapes and colors which may or may not have a peg. A peg is a cellulosic extension of the cell wall on which the crystalline material is deposited. Pegged cystoliths usually become stained (safranin and fast green), whereas the pegless cystoliths remain glassy to white-opaque even after staining (FIGURES 2, 3).

Mucilage refers to cellular contents which appear viscous to frothy in texture and vary in color from gray-green to pink when stained with safranin and fast green (FIGURE 4).

The terms loose and compact, as applied to the spongy mesophyll, refer to the relative amount of intercellular space. Also, a loose spongy mesophyll has relatively fewer cells per unit volume than a compact spongy mesophyll (FIGURES 5, 2).

The following leaf anatomical features occur throughout the entire family with exceptions listed: leaves are dorsiventral, the cuticle is less than five microns thick, the stomatal apparatus is anomocytic, and guard cells are elongate-reniform (FIGURE 6). Stomates are found only on the lower epidermis. Both upper and lower epidermis are uniseriate, except in *Trema amboinensis* and *T. orientalis* where the upper epidermis is 2 or 3 layers thick. The lower epidermis is papillate beneath major veins in the following genera: *Phyllostylon*, *Planera*, *Ulmus*, *Zelkova*, *Hemiptelea*, *Parasponia*, *Mirandaceltis*, *Gironniera*, and *Lozanella*. In most species of *Celtis* the entire lower epidermis is papillate. A parenchymatous bundle sheath surrounds both major and minor veins; however, surrounding some of the larger veins, there are also gelatinous thick-walled parenchyma cells.

Unicellular trichomes have a bulbous base (FIGURE 7) and occur on both the upper and lower epidermis. The walls are usually impregnated with silica. Multicellular hairs usually found on both leaf surfaces are of three basic types: the first found in some species of *Phyllostylon*, *Planera*, *Ulmus*, *Chaetoptelea*, *Celtis*, *Ampelocera*, *Zelkova*, *Hemiptelea*, *Trema*, *Aphananthe*, and *Lozanella* comprises a uniseriate linear row of

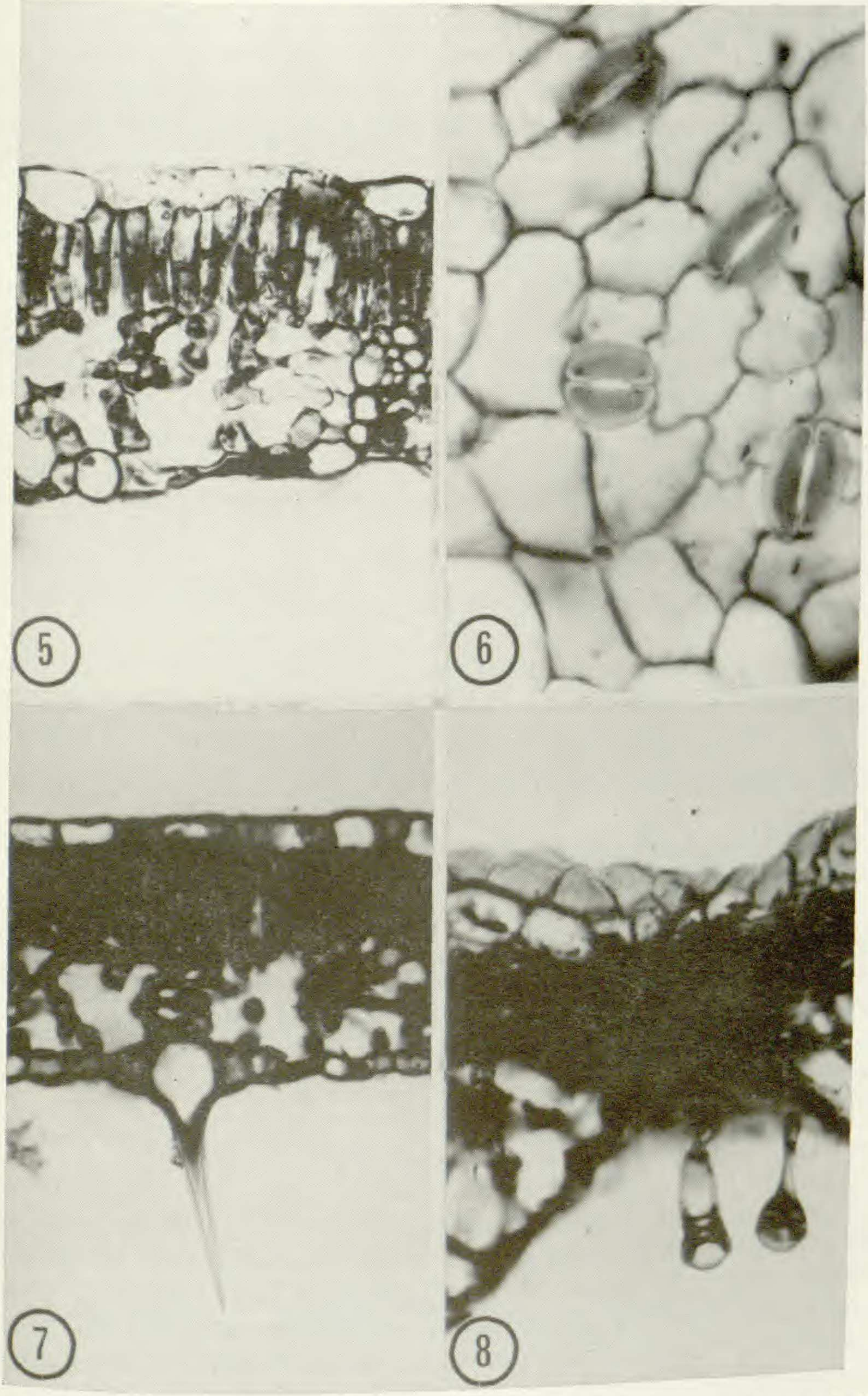


FIGURE 5, *Ulmus glabra.* Cross section of leaf with a loose spongy mesophyll, × 320. 6, *Pteroceltis tataranowii.* Paradermal section of leaf with an anomocytic stomatal apparatus and elongate reniform guard cells, × 400. 7, *Ulmus glabra.* Cross section of leaf with a bulbous-based unicellular hair, × 220. 8, *Ulmus rubra.* Cross section of leaf with two uniseriate multicellular trichomes, × 430.

cells (3–8) with the terminal cell and sometimes stalk cells being glandular, that is, containing dark staining material (FIGURE 8) and in addition some of the hairs are biseriate throughout their length in *Trema*. The second type has a uniseriate linear stalk of 3 to 8 cells but a multicellular glandular head of 2 to 4 cells and is found in some species of *Ulmus, Celtis, Ampelocera, Parasponia, Gironniera*, and *Lozanella* (FIGURE 9). The third type has a multicellular stalk with a single enlarged terminal cell in some species of *Ulmus* and *Trema* (FIGURE 10). Trichomes are usually associated with veins

Phyllostylon (2). Multicellular hairs found only on the lower epidermis; overall venation pattern brochidodromous, and terminal tracheids in areoles are surrounded by a parenchyma sheath. Leaf margin is serrate in *Phyllostylon rhamnoides* and entire in *P. brasiliensis*; palisade mesophyll is 1 to 4 cells deep, the spongy mesophyll is compact; bundle sheath extensions not well developed in *P. brasiliensis* but conspicuous in *P. rhamnoides*.

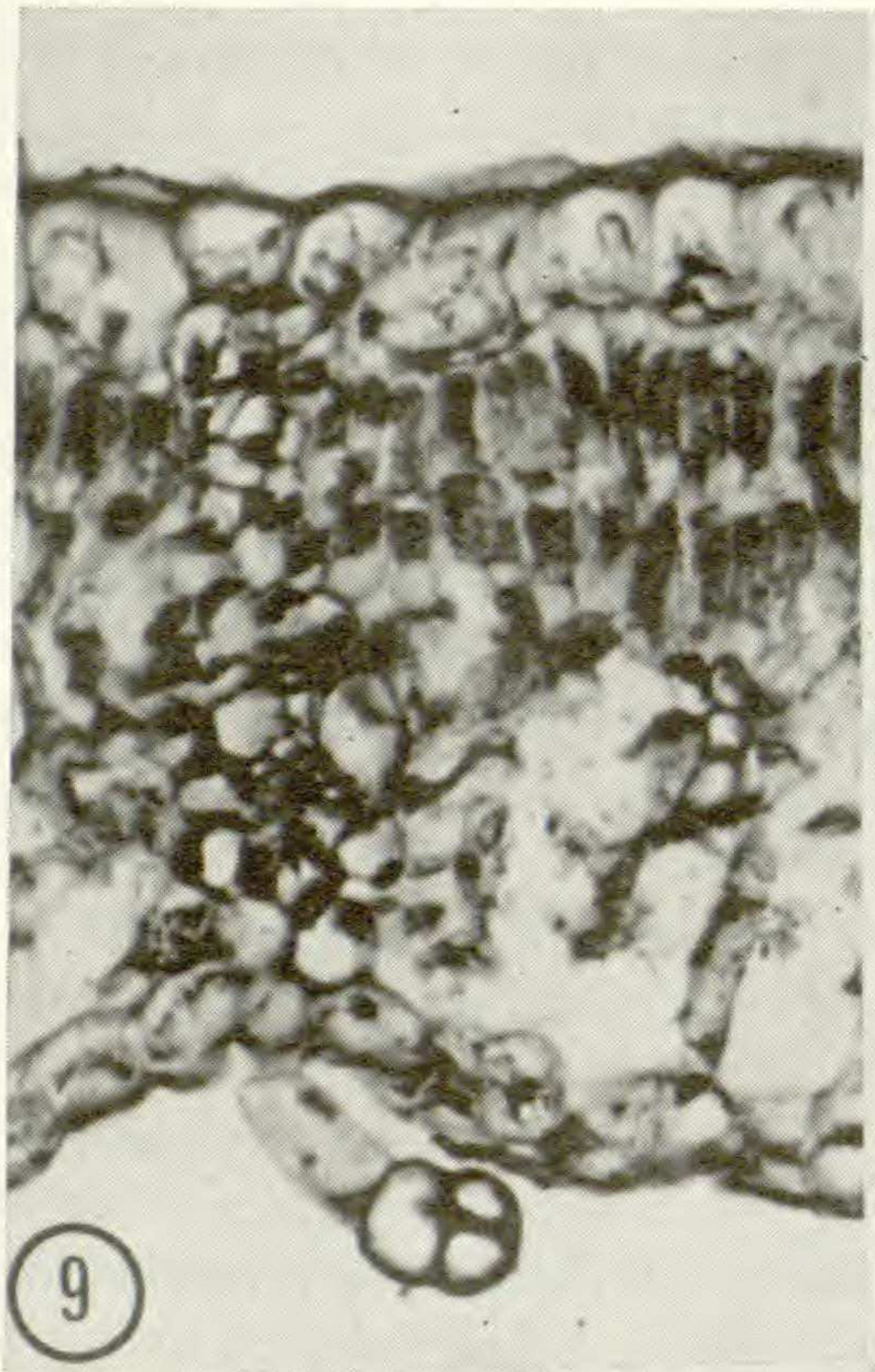
Cystoliths present in enlarged cells of both upper and lower epidermis in *P. rhamnoides*. There are about 60 per mm.^{2} in the upper epidermis and 40 per mm.^{2} in the lower epidermis. In *P. brasiliensis* they are only in the lower epidermis and number about 100 per mm.^{2} Druses are found in the mesophyll and phloem of both species; in addition, *P. rhamnoides* has prismatic crystals in the bundle sheath and phloem and styloids in all living tissues.

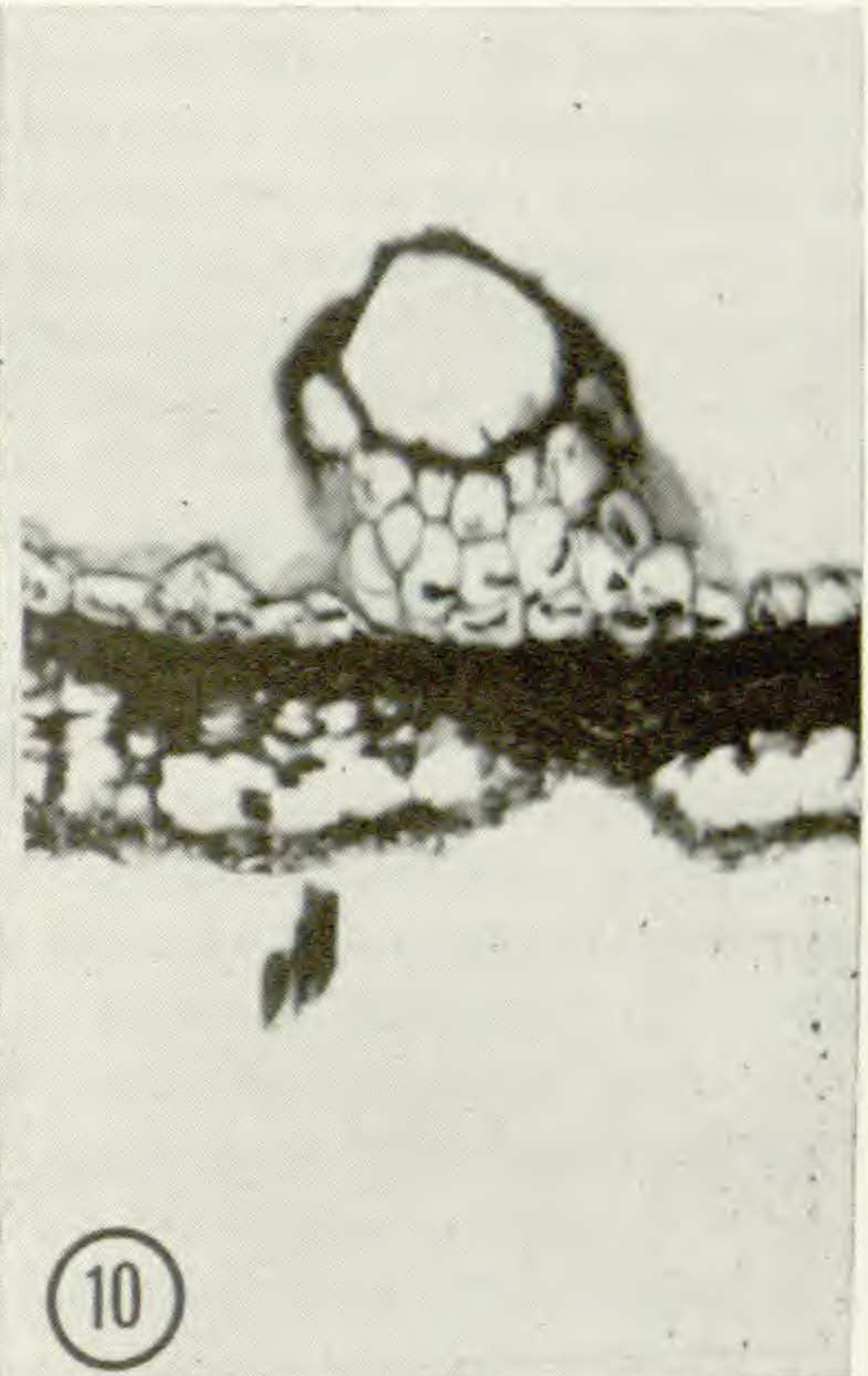
Holoptelea (1). Leaf margins are entire, the overall venation pattern is brochidodromous. In the areole, the veins terminate as individual tracheary elements without a sheath (FIGURE 11). A uniseriate palisade layer and a medium compact spongy layer are present. Chlorenchymatous bundle sheath present around both major and minor veins; chlorenchymatous bundle sheath extensions on both sides of major veins.

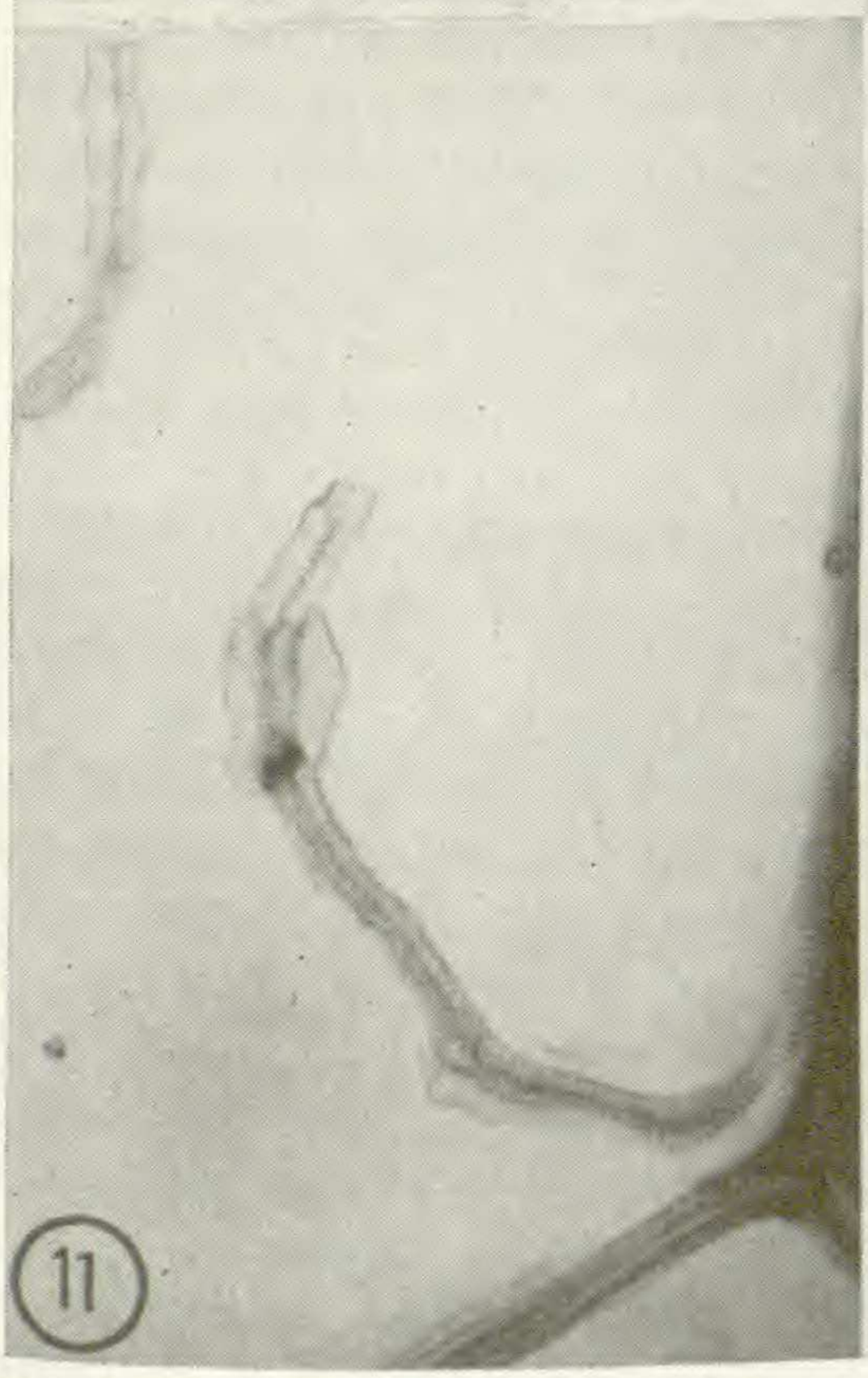
Cystoliths present in enlarged cells of the lower epidermis and in bases of unicellular hairs. Cystoliths approximately 30 per mm.^{2}; druses occurring in cells of upper and lower epidermis, mesophyll, and phloem.

Planera (1). Multicellular hairs on the lower epidermis only, leaf margins serrate, the overall venation pattern is "simply" craspedodromous; veins terminating in areoles as individual tracheary elements without a sheath; mesophyll composed of a palisade layer 1 or 2 cells thick and a loose spongy layer; a bundle sheath extension present on both sides of major veins; mineral placks present on upper epidermis; druses present in the mesophyll; styloids in cells of both mesophyll and epidermis.

Ulmus (15, 27). Multicellular trichomes found in all species except *U. americana, U. crassifolia, U. glabra, U. minor, U. laevis, U. parvifolia*, and *U. thomasii*. Leaves oblique at base, margins varying from simply to







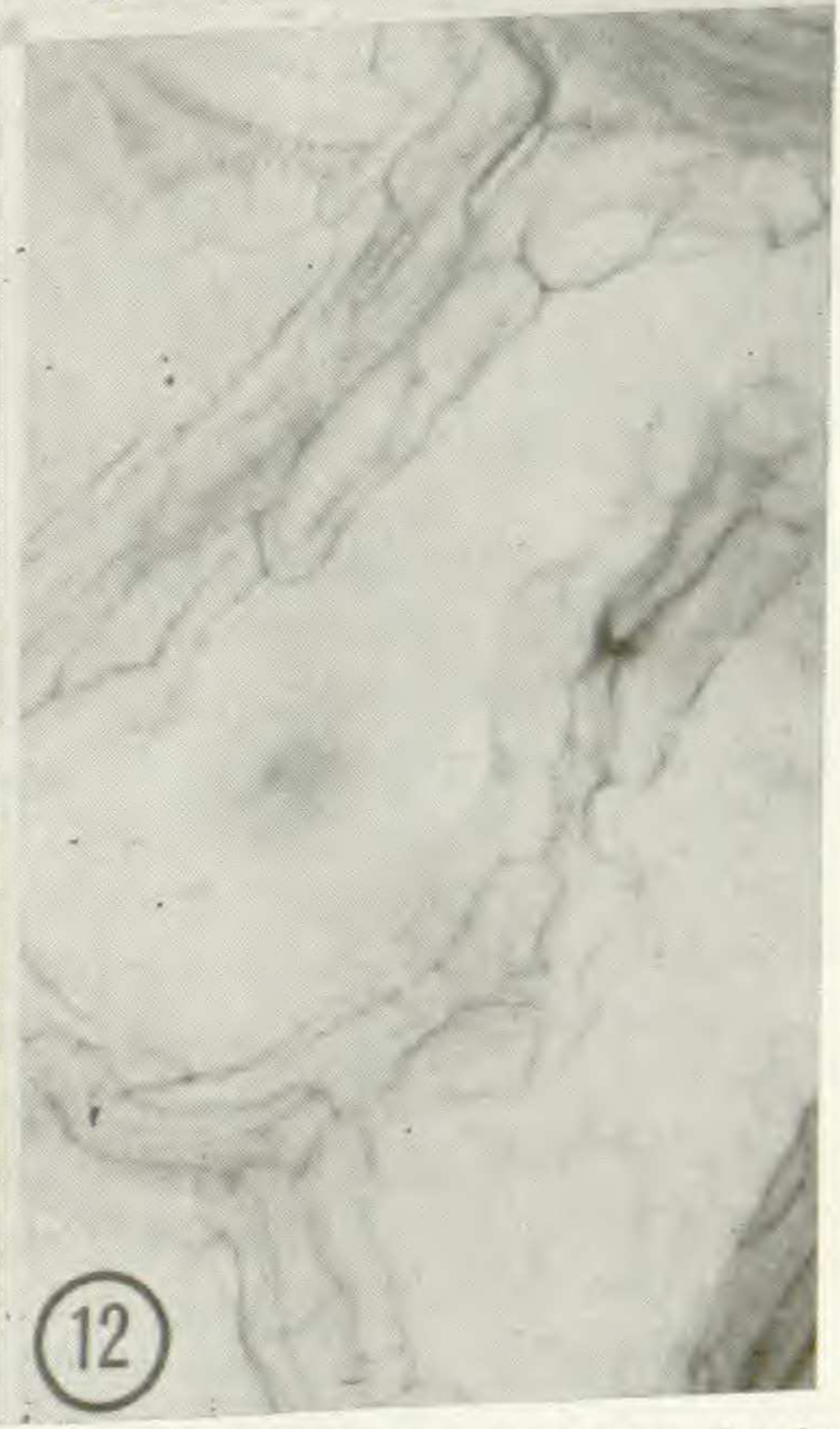


FIGURE 9, *Ulmus carpinifolia.* Cross section of leaf showing a short uniseriate stalked trichome with a multicellular head, × 400. 10, *Ulmus rubra.* Cross section of leaf with a multiseriate stalked hair with an enlarged terminal cell, × 250. 11, *Holoptelea integrifolia.* Clearing of leaf to show tracheary elements in the areole without bundle sheaths, × 300. 12, *Ulmus americana.* Clearing of leaf to show tracheary elements in the areole with a bundle sheath, × 300.

triply serrate; venation pattern is "simply" craspedodromous; terminal vein endings enclosed by a conspicuous parenchyma sheath within the areole (FIGURE 12); palisade mesophyll 1 to 4-seriate; the spongy mesophyll loose; bundle sheath extensions present on major veins.

Enlarged mucilage-containing cells occur in both upper and lower epidermal layers; mineral placks present in the upper epidermis. In several species, e.g., *U. parvifolia* and *U. glabra*, some upper epidermal cells below placks contain pegless cystoliths. Druses mostly in mesophyll and bundle sheath cells and to a lesser extent in cells of phloem and bundle sheath extensions; prismatic crystals commonly in the bundle sheath and phloem cells and to a lesser extent in cells of bundle sheath extensions; styloids present in cells of mesophyll and epidermis; mucilage-filled lacunae, resulting from cell disintegration found below midrib and other large veins in most species (FIGURE 13); these lacunae may be traumatic in origin.

Chaetoptelea (1). Leaf margin serrate, overall venation pattern is "simply" craspedodromous; in the areole, terminal tracheary elements are surrounded by a bundle sheath; mesophyll comprising a palisade layer of 1 or 2 cells and a loose spongy layer; bundle sheath extensions present only on major veins.

Mineral placks found covering clusters of cells in upper and lower epidermis; druses found in cells of mesophyll, bundle sheath, and bundle sheath extensions; prismatic crystals present in phloem, bundle sheath, and bundle sheath extension cells; styloids occurring in mesophyll and epidermal cells.

Celtis (17, 28). Multicellular trichomes occur only in *Celtis iguanaea*, *C. pubescens*, *C. reticulata*, and *C. sinensis*. The leaf margins vary from entire in *C. occidentalis* and *C. schippii* to serrate in *C. triflora* and *C. pumila*. Species with serrate margins have teeth mostly from the middle of the leaf to the tip. *Celtis laevigata*, *C. jessoensis*, and *C. reticulata* have oblique leaf bases. Overall venation pattern brochidodromous except in *C. philippinensis* where it is "perfect" actinodromous. Most species lack a parenchyma sheath around the terminal tracheary elements of the areole, except *C. caudata*, *C. jessoensis*, *C. philippinensis*, *C. schippii*, and *C. spinosa*. Palisade mesophyll has 1 to 3 layers, the spongy mesophyll is compact except in *C. pallida* where it is loose; bundle sheath extensions present on major veins except in *C. iguanaea* and *C. spinosa*.

Cuticular ridges on upper and lower epidermis of *C. occidentalis*, *C. pumila*, and *C. tournefortii*, and on lower epidermis only of *C. jessoensis*, *C. laevigata*, *C. reticulata*, *C. sinensis*, and *C. tenuifolia*. Upper epidermal anticlinal walls sinuous in most species; outer periclinal walls of upper epidermis thickened in *C. laevigata*, *C. pallida*, *C. reticulata*, and *C. tournefortii*.

Pegged cystoliths present in enlarged upper and lower epidermal cells and in unicellular hairs, these present only in the upper epidermis of *C. laevigata*, *C. occidentalis*, *C. philippinensis*, *C. pubescens*, *C. pumila*, *C. sinensis*, *C. tenuifolia*, and *C. tournefortii*, and in the upper and lower epidermis of all other species. Pegless cystoliths found in enlarged upper and lower epidermal cells of *C. schippii*; the number of cystoliths per mm.^{2} ranging from 40 to 148 in the upper epidermis and from 0 to 48 in the lower epidermis.

Prismatic crystals present in bundle sheaths of most specimens and in phloem of *C. caudata*, *C. iguanaea*, and *C. spinosa*; no prismatic crystals present in *C. pallida*, *C. schippii*, and *C. trinervia*; styloids found in living cells of all tissues of *C. pallida*; mucilage not found in *C. iguanaea*, *C. spinosa*, or *C. trinervia*.

Pteroceltis (1, 2). Leaf margin serrate and overall venation pattern brochidodromous; terminal tracheary elements surrounded by a sheath of round to oval cells; mesophyll divided into a palisade layer (1 or 2-seriate) and a loose spongy layer; major veins with bundle sheath extensions.

Pegged and unpegged cystoliths occurring in enlarged cells and hairs of the upper and lower epidermis; cystoliths in distinctive clusters of 20 (±) cells, usually surrounding a trichome; druses found in cells of the mesophyll, bundle sheath, bundle sheath extension, and phloem; styloids present in the mesophyll.

Ampelocera (3). Multicellular hairs occurring on the lower epidermis of *Ampelocera cubensis*; short stalked hairs with a glandular, multicellular capitate head occurring in indentations of upper and lower epidermis of *A. hottlei* (FIGURE 14). No multicellular hairs found on *A. edentula*.

Leaf margin entire and leaf base slightly oblique; overall venation pattern brochidodromous; terminal tracheary elements having a sheath in *A. hottlei*, but not in *A. cubensis* or in *A. edentula*. Palisade mesophyll with 1 or 2 layers, the spongy mesophyll varying from loose in *A. hottlei* to compact in *A. cubensis*; bundle sheath extensions found only in *A. cubensis*.

Pegged cystoliths in enlarged cells of the upper epidermis of all species (1 to 40 per mm.^{2}) and in the lower epidermis of *A. hottlei* (12 per mm.^{2}); druses in the mesophyll, bundle sheath, and phloem of *A. hottlei*; prismatic crystals in bundle sheaths of *A. edentula* and *A. hottlei* and also in phloem of the latter; styloids in living cells of all tissues in *A. cubensis*.

Zelkova (3, 4). Leaves with an oblique base and serrate margins; overall venation pattern "simply" craspedodromous and tracheary elements in the areole surrounded by a parenchyma sheath; mesophyll with 1 or 2 palisade layers and a loose spongy layer; major veins with bundle sheath extensions.

Pegless cystoliths in upper and lower epidermal cells; mineral placks

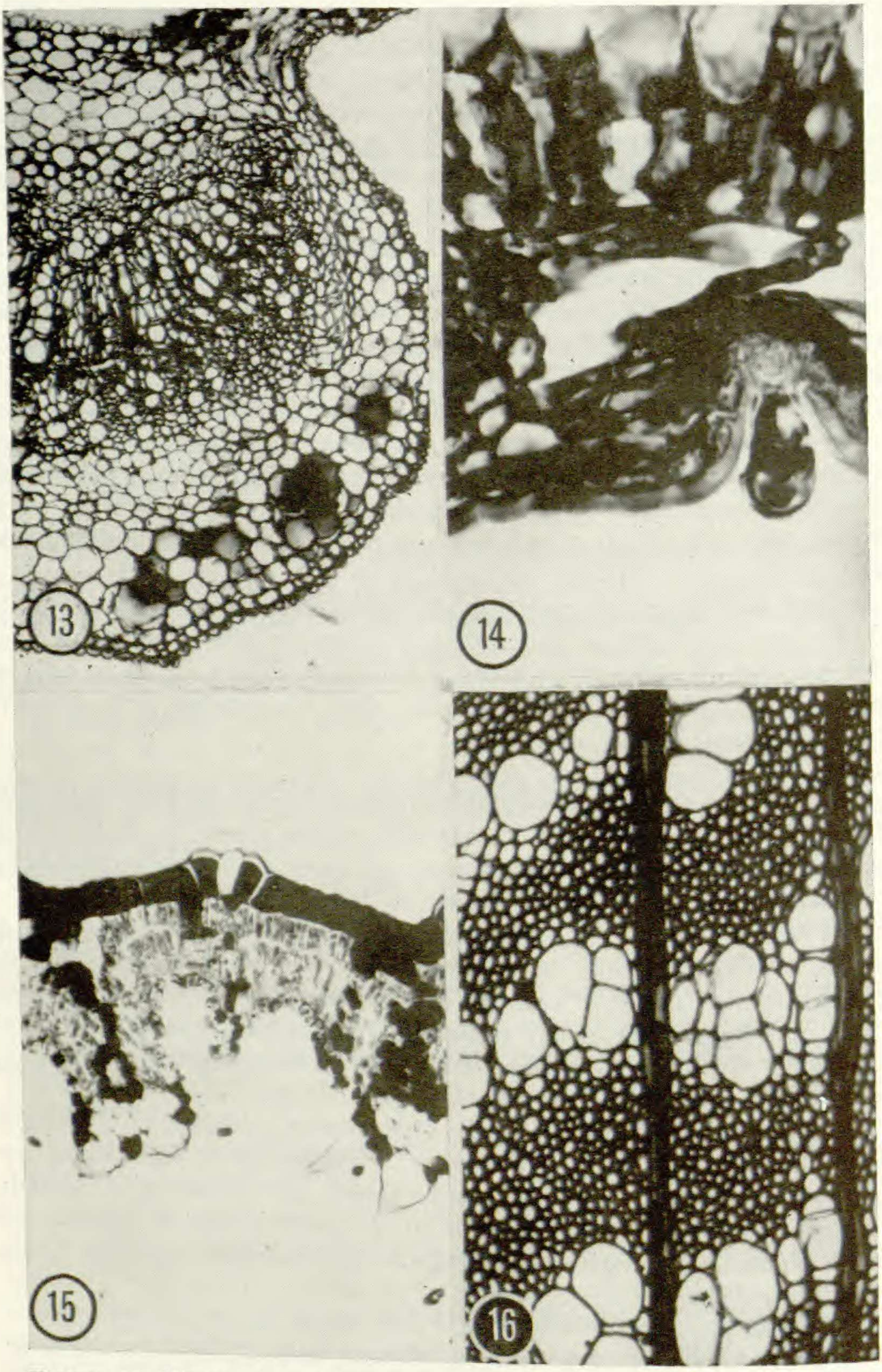


FIGURE 13, *Ulmus rubra*. Cross section of midrib of a leaf showing mucilage-filled cavities, × 140. 14, *Ampelocera hottlei*. Cross section of leaf with a multicellular hair in an indentation of the lower epidermis, × 450. 15, *Trema lamarckiana*. Cross section of leaf illustrating the uneven lower epidermis, × 110. 16, *Ulmus americana*. Transverse wood section illustrating the tangential (wavy) pore arrangement, × 120.

on the upper epidermis; prismatic crystals in the phloem, bundle sheath, and bundle sheath extensions; styloids in all living tissues of *Zelkova carpinifolia* and *Z. sinica*.

Hemiptelea (1, 2). Multicellular hairs on the lower epidermis; leaf margins serrate, the overall venation pattern "simply" craspedodromous; terminal tracheary elements in the areole surrounded by a sheath; two or three palisade layers and a loose to medium compact spongy layer; bundle sheath extensions on upper and lower sides of major veins.

Pegged cystoliths in upper and lower epidermis; in upper epidermis cystoliths arranged in groups with a unicellular hair in the center (32 to 120 cystoliths per mm.^{2}); cystolith groups abundant and easily visible to the unaided eye, appearing as dark spots on leaf surface; on the lower epidermis 1 to 20 cystoliths per mm.^{2} Druses occurring in cells of phloem, mesophyll, bundle sheath, and bundle extension; styloids present in living cells of all tissues.

Trema (5). Multicellular trichomes comprising a linear row of cells on both leaf surfaces of all species except in *Trema amboinensis* and *T. canescens* occurring only on the lower epidermis. Multicellular stalked trichomes with an enlarged terminal cell on both surfaces of *T. lamarckiana*, *T. micrantha*, and *T. orientalis*.

Leaves with an entire margin, overall venation pattern "perfect" acrodromous in *T. canescens*, and "imperfect" acrodromous for all other species; terminal tracheary elements in the areole lacking a bundle sheath; mesophyll is divided into 1 to 4 palisade layers; a loose spongy layer present (except compact in *T. amboinensis* and variable in *T. lamarckiana*; bundle sheath extensions present on major veins.

Lower epidermis quite uneven in most species due to prominent ridges and valleys formed by veins (FIGURE 15); *Trema orientalis* with cuticular ridges on both epidermal layers; pegged cystoliths present in enlarged cells and in unicellular hairs of the upper and lower epidermis of *Trema lamarckiana* and *T. micrantha* but only in the upper epidermis of *T. amboinensis*, *T. canescens*, and *T. orientalis*. Cystoliths per mm.^{2} ranging from 27 to 48 for the upper epidermis and from 13 to 16 for the lower; druses found in mesophyll, bundle sheath, bundle sheath extension, and phloem cells; prismatic crystals in phloem and bundle sheath; styloids in living cells of all tissues in *T. micrantha*.

Parasponia (1). Leaf margins serrate and overall venation pattern "simply" craspedodromous; terminal tracheary elements in the areole lacking a bundle sheath; mesophyll divided into a uniseriate layer and a loose spongy layer; bundle sheath extensions poorly developed or lacking.

Pegged cystoliths found in enlarged cells and hairs of both the upper and lower epidermis (10 per mm.^{2} in the upper epidermis and 35 per mm.^{2} in the lower); druses present in the cells of the mesophyll, bundle sheath, and phloem; mineral placks covering several cells in both upper and lower epidermis.

Aphananthe (2). Unicellular hairs barbed; leaf margins serrate, overall venation pattern "simply" craspedodromous in *Aphananthe aspera* and brochidodromous in *A. philippinensis*; terminal tracheary elements in the areole without a sheath; mesophyll with 1 or 2 palisade layers and a loose spongy layer; major veins have bundle sheath extensions.

Pegless cystoliths found in enlarged cells of both upper and lower epidermis; druses in cells of the mesophyll, bundle sheath, and phloem; *Aphananthe philippinensis* with prismatic crystals in the bundle sheath, bundle sheath extension, and phloem; mineral placks in both upper and lower epidermis.

Mirandaceltis (1, 2). Some unicellular hairs barbed; leaves with entire margin and overall venation pattern brochidodromous; terminal tracheary elements lacking bundle sheath in the areole; mesophyll divided into 1 or 2 palisade layers and a tight spongy layer; bundle sheath extensions either absent or weakly developed.

Periclinal walls of the upper epidermis, and to a lesser extent of the lower, thickened; pegless cystoliths present in enlarged cells or hairs on upper epidermis; druses present in cells of mesophyll, bundle sheath, and phloem; prismatic crystals found in the two latter tissues; styloids found in the mesophyll.

Gironniera (5). *Gironniera parvifolia* and *G. nervosa* with some barbed unicellular hairs; multicellular trichomes on lower epidermis only in *G. nervosa*.

Leaf margins entire and overall venation pattern brochidodromous; terminal trachery elements in the areoles surrounded by round to oval parenchyma cells; mesophyll divided into 1 or 2 palisade layers and a loose spongy layer; major veins with a bundle sheath extension.

Pegless cystoliths in enlarged cells of lower epidermis; druses found in cells of mesophyll, bundle sheath, bundle sheath extension, and phloem; prismatic crystals found in cells of the bundle sheath, bundle sheath extension, and phloem of *G. cuspidata*, *G. nervosa*, and *G. nitida*; styloids in mesophyll and epidermal cells of *G. nervosa*.

Chaetachme (1). Leaf margin entire, overall venation pattern brochidodromous; terminal tracheary elements in the areole surrounded by a bundle sheath; mesophyll divided into 1 or 2 palisade layers and a loose spongy layer; bundle sheath extensions occurring only from major veins.

Enlarged cells containing mucilage in upper epidermis; druse and prismatic crystals found in bundle sheaths.

Lozanella (1). Leaf margin serrate, overall venation pattern brochidodromous; terminal tracheary elements surrounded by a parenchyma sheath in the areole; mesophyll composed of 1 or 2 palisade layers and a loose spongy layer; major veins with bundle sheath extensions.

Cuticular ridges present on both upper and lower epidermis; pegless cystoliths in enlarged cells and in hairs of both upper and lower epidermis; druses in cells of the mesophyll, bundle sheath, and phloem.

Wood

Secondary xylem of Ulmaceae is variable, but the following features are common to all members. Vessel elements ligulate to eligulate; inter-vascular pitting alternate, pits elongate to circular in outline; fibers with simple to slightly bordered slit-like pits. Unilaterally compound pitting common between both axial and ray parenchyma and vessel elements. Pores angular to circular; vascular rays uniseriate, biseriate, and multiseriate; ray cells thick walled in all species.

Phyllostylon (1). Wood diffuse porous; pore distribution 79 percent solitary, 19 percent radial multiples of 2 to 4 cells, and 2 percent clusters of 3 cells; average pore diameter 53 μ with a range of 35 to 70 μ; vessel element wall thickness from 1.5 to 4 μ; perforations simple; end wall angles from 57 and 90°; inter-vascular pits ranging in diameter from 6 to 7 μ; average length of vessel elements 187 μ with a range of 135 to 240 μ; fiber wall thickness from 4.5 to 5.5 μ; average fiber length 903 μ with a range of 690 to 1215 μ.

All vascular rays homocellular and comprised of procumbent cells; uniseriate rays ranging in height from 3 to 11 cells and from 45 to 200 μ; biseriate and multiseriate rays ranging in height from 7 to 65 cells and from 100 to 900 μ, and ranging in width from 2 to 4 cells and from 15 to 35 μ; prismatic crystals observed in some ray cells.

Axial parenchyma vasicentric and confluent; vessel-ray and vessel-axial parenchyma pitting alternate, pits ranging in diameter from 2.5–5 μ

Holoptelea (2, 3). All woods diffuse porous; pore distribution is 61 to 80 percent solitary, 18 to 35 percent radial multiples of 2 to 4 cells, and 2 to 4 percent clusters of 3 to 11 cells; average pore diameters ranging from 92 to 110 μ, the total range of diameters from 50 to 170 μ; wall thickness of vessel elements ranging from 2.5 to 3.5 μ; perforations simple; end wall angles of vessel elements ranging from 40 to 90°; tyloses in vessel elements of *H. grandis*; average vessel element length ranging from 273 to 284 μ, the total range of lengths from 148 to 370 μ.

Fiber wall thickness from 2 to 3.5 μ; average fiber length from 1169 to 1428 μ with a total range of lengths from 925 to 1702 μ.

Homocellular uniseriate, biseriate, and multiseriate vascular rays comprised of procumbent cells; uniseriate rays few in comparison with the storied biseriate and multiseriate rays. Uniseriate rays ranging in height from 2 to 12 cells and from 60 to 225 μ; biseriate and multiseriate rays ranging in height from 6 to 57 cells and from 95 to 750 μ; width of rays from 2 to 5 cells and from 10 to 55 μ.

Axial parenchyma vasicentric, aliform, and confluent in all specimens; pitting of vessel-ray and vessel-axial parenchyma alternate, pit diameters ranging from 2.5 to 6 μ.

Planera (1, 3). Two specimens of *Planera aquatica* (USw21789 and Yw6699) diffuse porous; Yw11169 ring porous. Pore distribution 32 to 40 percent solitary, 18 to 35 percent radial multiples of 2 to 4 cells, and 39 to 46 percent clusters of 3 to 9 cells. Average pore diameter 38 μ for the diffuse porous specimens, with a total range of 20 to 55 μ. Average pore diameter of 34 μ for the ring porous specimen and a range from 20 to 55 μ for the early portion of the ring, an average pore diameter of 25 μ and a range from 20 to 35 μ for the last formed portion of the ring. Vessel wall thickness from 0.5 to 3 μ; perforations simple in all three specimens; however, vestigial bars also occurring in the ring porous specimen. End wall angles of vessel elements varying from 24 to 90°; intervascular pit diameters from 5 to 7 μ; average vessel element length from 180 to 450 μ; all vessel elements usually with spiral thickenings.

Imperforate tracheary elements comprised of fiber-tracheids with slightly to prominently bordered pits and vascular tracheids; many vascular tracheids have spiral thickenings. Average lengths of fiber-tracheids from 817 to 885 μ; total range of lengths from 375 to 1485 μ. Some storying of fiber-tracheids occurs in Yw11169.

Vascular rays homocellular; uniseriate rays ranging in height from 2 to 19 cells and from 50 to 400 μ; biseriate and multiseriate rays ranging in height from 5 to 63 cells and from 85 to 1135 μ are from 2 to 6 cells and from 15 to 75 μ in width; prismatic crystals observed in some ray cells, which are sometimes enlarged.

Axial parenchyma diffuse, banded, terminal, and vasicentric; crystals and dark staining contents observed in some axial parenchyma cells; vessel-ray pitting and vessel-axial parenchyma pitting alternate, pits ranging in diameter from 2 to 3 μ.

Ulmus (33, 55). Wood specimens examined ring porous; pores often oriented in wavy tangential lines (FIGURE 16); pore clusters and solitary pores most numerous and radial multiples the least prevalent type of pore distribution; decrease in percentage of clusters usually correlated with a corresponding increase in percentage of solitary pores, little or no change occurring in the percentage of radial multiples; solitary pore distribution from 14 percent in *Ulmus wallichii* to 63 percent in *U. pumila* var. *arborea*; clusters from 32 percent in the latter species to 81 percent in *U. montana*. In *U. canescens*, *U. carpinifolia*, *U. laevis*, *U. macrocarpa*, *U. parvifolia*, *U. pumila*, *U. rubra*, *U. sieboldii*, and *U. uyematsii* no radial multiples occur; in *U. americana* radial multiples accounted for 16 percent of the pore distribution. Number of cells per radial multiple from 2 to 4 and the number per cluster from 3 to 28.

Average pore diameter ranges from 53 μ in *U. pumila*, to 211 μ in *U. glabra* in the first formed portion of the ring, and from 19 μ in *U. rubra* to 53 μ in *U. major* in the last formed portion; vessel wall thickness ranges from 1.5 to 8 μ.

Mostly simple perforations in all species; *Ulmus laevis, U. major, U. rubra, U. serotina,* and *U. stricta* having scalariform perforation plates with one bar (FIGURE 17); *Ulmus alata, U. americana, U. crassifolia, U. glabra, U. hollandica* var. *major, U. laevis, U. macrocarpa, U. major, U. procera, U. pumila, U. rubra, U. scabra, U. serotina, U. stricta, U. thomasii,* and *U. wallichii* having vestigial bars on perforation plates. Only vessel elements of small diameters with vestigial bars or scalariform perforations (FIGURE 18); vessel element end wall angles from 18 to 90°; most species with at least some vessels with 90° end walls; in general, the greater the diameter of the vessel element, the closer the end wall angle to 90°.

Ulmus alata, U. carpinifolia var. *suberosa, U. glabra, U. laciniata, U. macrocarpa, U. nitens, U. rubra, U. scabra,* and *U. stricta* all with some opposite intervascular pitting; diameters of the intervascular pits from 5.5 to 10 μ.

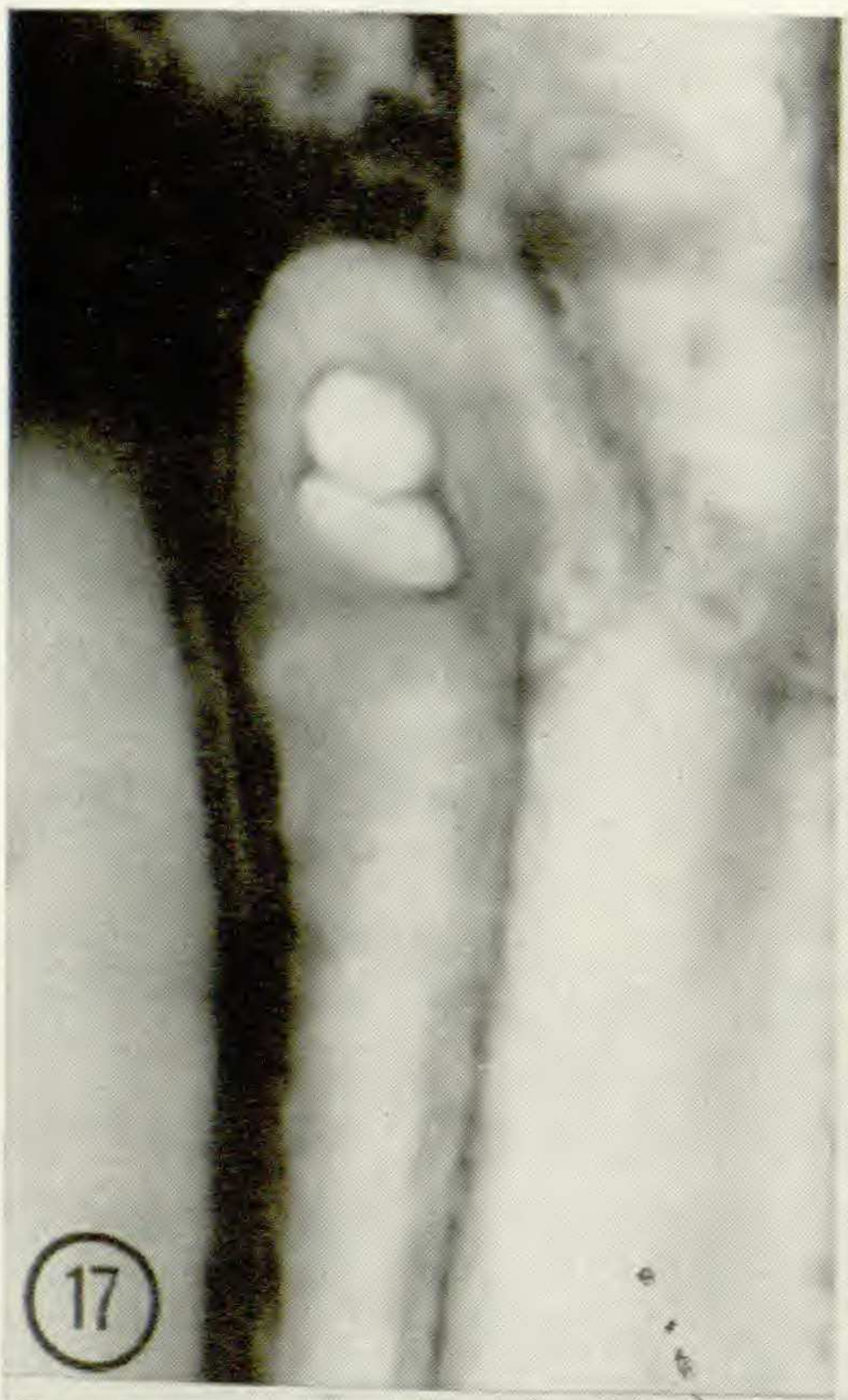
Average vessel element lengths range from 170 μ in *U. thomasii* to 381 μ in *U. major*; the range of all vessel element lengths varying from 111 to 481 μ; tyloses found only in *U. crassifolia* and *U. scabra.*

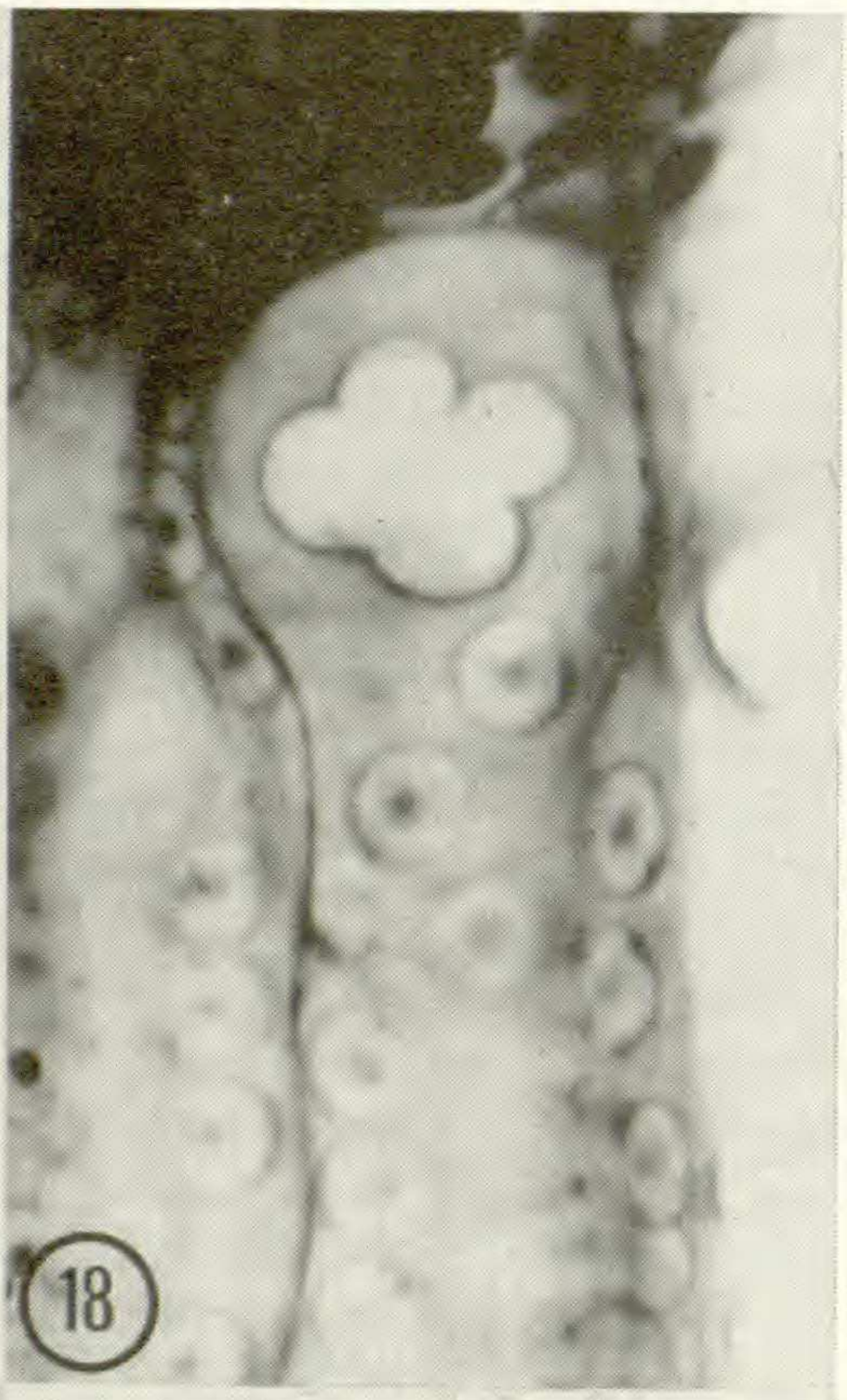
Imperforate tracheary elements include vascular tracheids and fibers; wall thickness of fibers ranges from 1.5 to 5.5 μ; average lengths of fibers range from 779 μ in *U. carpinifolia* to 1782 μ in *U. montana*; total range of lengths for all specimens is 660 to 2146 μ.

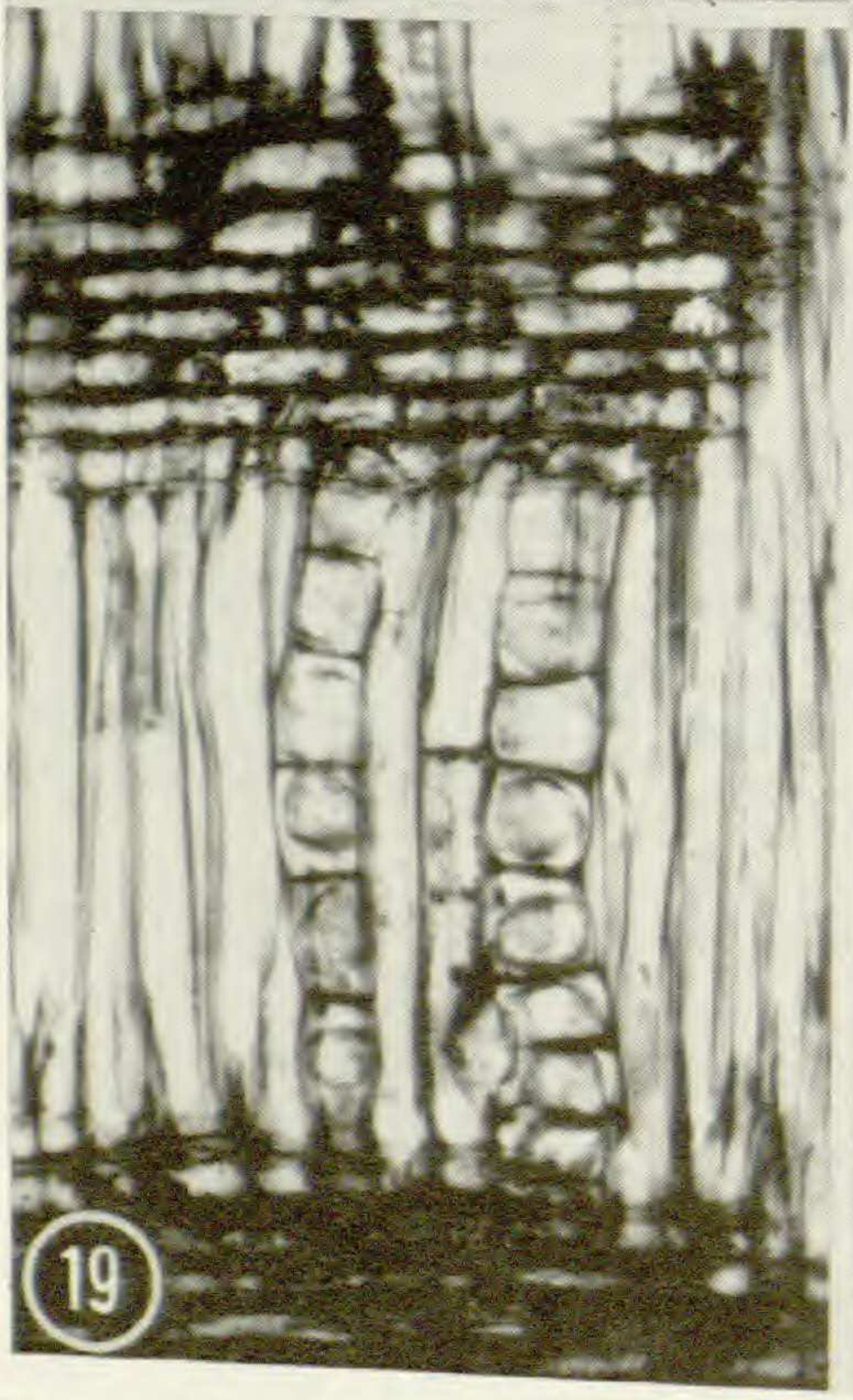
Vascular rays of all species homocellular, comprised of procumbent cells; unicellular rays ranging in height from 2 to 21 cells and from 20 to 230 μ. Biseriate and multiseriate rays ranging in height from 3 to 76 cells and from 50 to 1375 μ; these rays ranging in width from 2 to 19 cells and from 10 to 200 μ; vessel-ray pitting mostly alternate; however, species with some opposite pitting are: *U. alata, U. carpinifolia* var. *suberosa, U. glabra, U. hollandica* var. *major, U. macrocarpa, U. major, U. nitens, U. rubra, U. scabra,* and *U. stricta.* Diameter of vessel-ray pits ranges from 2.5 to 5 μ.

Axial wood parenchyma mostly vasicentric with some aliform in *U. crassifolia* and some confluent in *U. alata, U. americana, U. scabra,* and *U. thomasii,* most species showing terminal axial parenchyma. Vessel-axial parenchyma pitting mostly alternate with some opposite in *U. alata, U. carpinifolia* var. *suberosa, U. glabra, U. laciniata, U. macrocarpa, U. major, U. nitens, U. plotii, U. rubra, U. scabra, U. serotina, U. stricta, U. suberosa,* and *U. thomasii.*

Storying of vessel elements and some fibers occurs in *U. alata, U. glabra, U. scabra,* and *U. serotina.* Prismatic crystals present in ray cells of *U. americana, U. major, U. montana, U. plotii, U. rubra, U. scabra, U. sieboldii, U. thomasii,* and *U. uyematsii*; prismatic crystals in enlarged axial parenchyma cells of *U. laciniata, U. major,* and *U. scabra.* Strands of







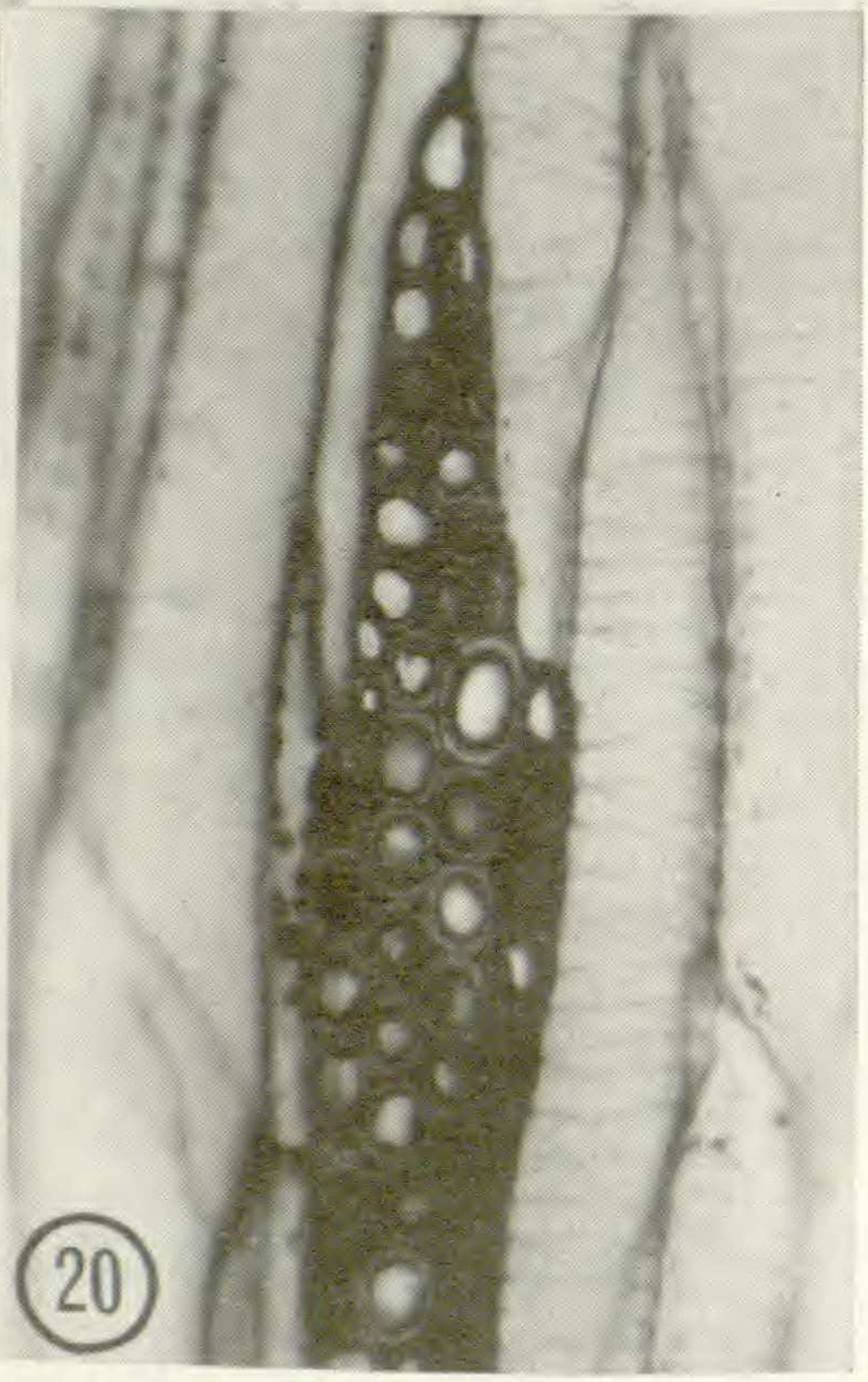


FIGURE 17, *Ulmus serotina*. Radial wood section illustrating a scalariform perforation plate with one bar, × 730. 18, *Ulmus serotina*. Radial wood section showing a perforation plate with vestigial bars, × 730. 19, *Ulmus major*. Radial wood section with crystal strands, × 200. 20, *Ulmus rubra*. Tangential wood section with spiral thickenings on the walls of the vessel elements, × 330.

parenchyma containing prismatic crystals (FIGURE 19) in all species except *U. laciniata*, *U. montana*, *U. procera*, *U. scabra*, and *U. stricta*. Dark staining deposits in many vascular ray cells and axial wood parenchyma cells.

Spiral thickenings on the walls of small vessels and vascular tracheids of all species (FIGURE 20).

Chaetoptelea (1, 2). The names *Chaetoptelea mexicana* Liebm. and *Ulmus mexicana* (Liebm.) Planch. are synonymous; some botanists recognizing *Chaetoptelea* as a distinct genus and others not. For this reason, specimens bearing both binomials are treated in the same section here under *Chaetoptelea*.

Wood ring porous; pore distribution 80 percent solitary, 12 percent radial multiples of 2 to 4 cells, and 8 percent clusters of 3 or 4 cells. Average pore diameters for the first formed portion of the growth ring 150 μ with a range of 25 to 215 μ. Average pore diameters for the last formed portion of growth ring 90 μ, with a range of 40 to 200 μ; vessel wall thickness from 1 to 7 μ; perforations simple; end wall angles range from 44 to 90°; intervascular pit diameters from 3.5 to 6.5 μ. Average vessel element length is 300 μ with a total range of 148 to 407 μ; tyloses found in *C. mexicana*.

Imperforate tracheary elements include vascular tracheids and fibers. Fiber wall thickness from 1 to 3 μ; average fiber length is 1660 μ with a total range of 1221 to 2072 μ.

Vascular rays homocellular, comprised of procumbent cells. Uniseriate rays ranging in height from 2 to 7 cells and 25 to 120 μ. Biseriate and multiseriate rays ranging in height from 4 to 48 cells and 60 to 725 μ, in width from 2 to 8 cells and 15 to 75 μ. Dark staining materials found in some ray cells.

Axial parenchyma vasicentric, aliform, confluent, and terminal; vessel-ray and vessel-axial parenchyma pitting alternate; pits ranging in diameter from 3.5 to 6.5 μ; prismatic crystals and dark staining deposits in some ray cells; crystalliferous strands present.

Celtis (40, 50). Wood ring porous in *Celtis australis*, *C. bungeana*, *C. jessoensis*, *C. koraiensis*, *C. laevigata*, *C. lindheimeri*, *C. occidentalis*, *C. pumila*, *C. reticulata*, *C. sinensis*, *C. tenuifolia*, *C. tournefortii*, and *C. yunnanensis*, diffuse porous in *C. adolphi-friderici*, *C. asperifolia*, *C. cinnamomea*, *C. crenato-serrata*, *C. harperi*, *C. iguanaea*, *C. kraussiana*, *C. latifolia*, *C. luzonica*, *C. pacifica*, *C. pallida*, *C. paniculata*, *C. philippinensis*, *C. rigescens*, *C. ritiensis*, *C. schippii*, *C. soyauxii*, *C. swartzii*, *C. tala*, *C. trinervia*, *C. ugandensis*, *C. wightii*, and *C. zenkeri*. The genus may be divided into two groups based upon pore distribution and porosity; ring porous species having 42 to 85 percent solitary pores, 14 to 52 percent clusters of 3 to 30 cells, and 0 to 12 percent radial multiples of 2 to 4 cells (FIGURE 21). Diffuse porous species have 59 to 90 percent solitary pores, 9 to 49 percent radial multiples of 2 to 10 cells, and 0 to 6 percent clusters of 3 to 8 cells (FIGURE 22).

Pore diameters for the early part of the growth ring in ring porous species range from 58 to 191 μ with a total range of 20 to 265 μ; for the last formed portion of the ring diameters range from 20 to 40 μ with a total range of 15 to 100 μ. Average pore diameters for diffuse porous species range from 49 to 169 μ with a total range of 15 to 225 μ; vessel element wall thickness ranges from 1.5 to 6 μ; all diffuse porous species having only simple perforations; all ring porous species, except *Celtis lindheimeri* with exclusively simple perforations, having at least some perforations with vestigial bars in addition to simple perforations; *Celtis jessoensis*, *C. laevigata*, and *C. pumila* also having scalariform plates with one bar in addition to the vestigial bars; end wall angles varying from 10 to 90°; all species having at least some vessels with 90° end walls.

Celtis bungeana and *C. reticulata* with some opposite intervascular pitting; pitting crowded in *C. iguanaea*, *C. kraussiana*, *C. pacifica*, *C. philippinensis*, and *C. wightii*; intervascular pit diameters ranging from 2 to 9 μ; average vessel element lengths ranging from 170 to 455 μ; total range of lengths 111 to 666 μ; tyloses found in *C. iguanaea*, *C. laevigata*, *C. lindheimeri*, *C. reticulata*, and *C. ritiensis*.

Vascular tracheids present in ring porous species, absent in diffuse porous species; fiber wall thickness ranging from 1 to 5.5 μ; average fiber length range is 717 to 1709 μ with a total range of 518 to 2220 μ.

It is difficult to determine whether the uniseriate rays are homocellular, heterocellular, or both; in tangential section some of the component cells appear upright, but in radial section all cells are procumbent, radial dimensions exceeding the axial dimensions. There is a problem in correlating the appearance of a ray in radial section with its appearance in tangential section; however, if these so-called "upright" cells in tangential view were truly upright, they would not have been so scarce in radial section. Therefore, the uniseriate rays will be designated homocellular, even though some may be technically heterocellular. Whenever a similar condition is encountered in other genera, for the sake of uniformity in this paper such a uniseriate ray type is referred to as the Celtis type. Some multiseriate rays classed as heterocellular are conceivably homocellular, but a detailed statistical analysis of the cellular composition of rays from tangential and radial sections is beyond the scope of this paper.

Biseriate and multiseriate rays heterocellular with procumbent cells in the body of the ray and upright cells on the margins; height of unicellular rays from 2 to 25 cells and 20 to 1000 μ for all species; height of biseriate and multiseriate rays ranging from 3 to 115 cells and 40 to 1800 μ, width ranging from 2 to 14 cells and 10 to 195 μ. Two species, *Celtis kraussiana* and *C. laevigata*, showed a tendency towards formation of sheath ray cells since some of the marginal cells are elongated.

Vessel-ray parenchyma pitting and vessel-axial parenchyma pitting are considered together since they are similar in arrangement and size. All species investigated show what can be called alternate pit arrangement,

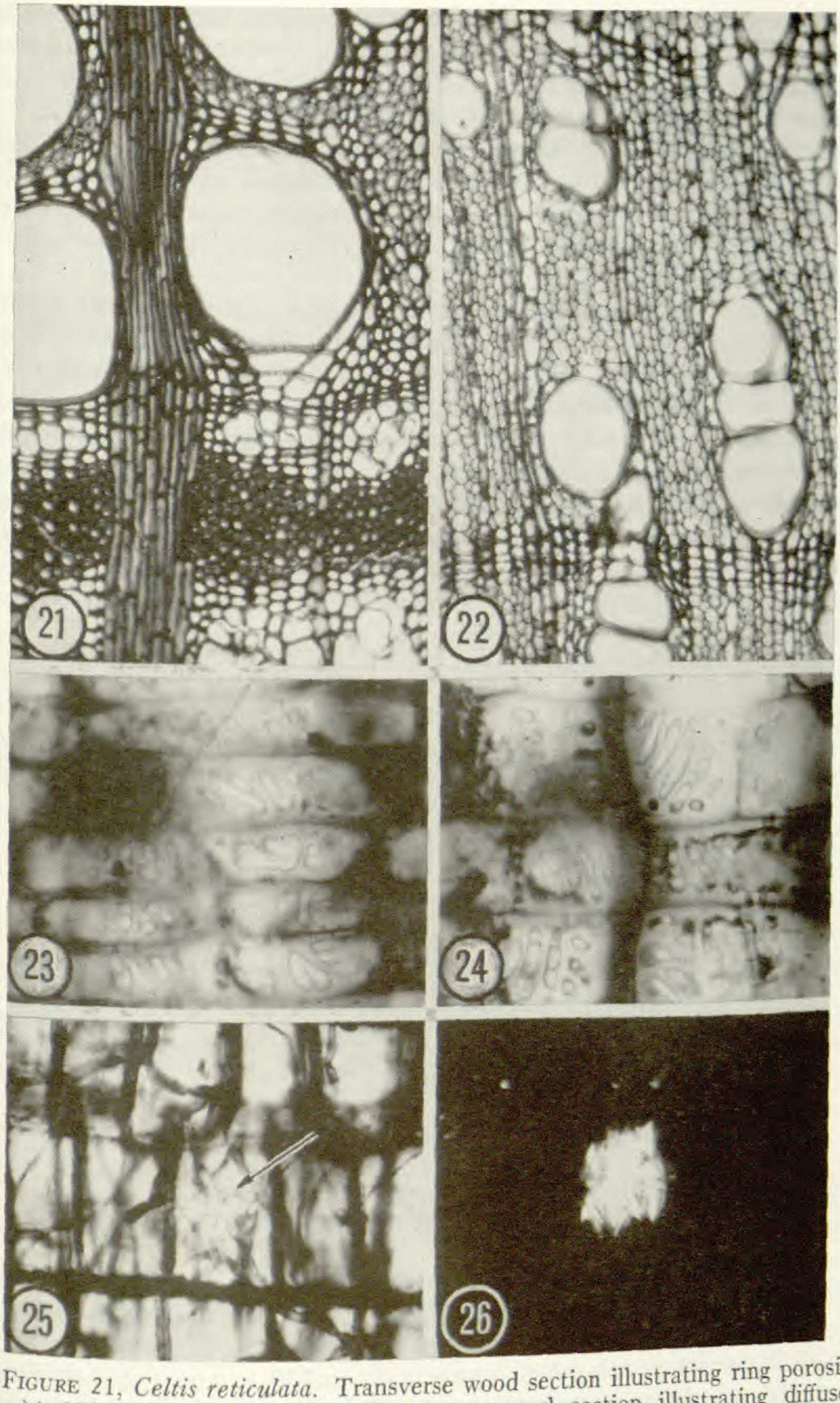


FIGURE 21, *Celtis reticulata*. Transverse wood section illustrating ring porosity, × 120. 22, *Celtis pallida*. Transverse wood section illustrating diffuse porosity, × 220. 23 and 24, *Celtis pacifica*. Radial wood sections illustrating variable vessel-ray pitting, × 660. 25, *Lozanella enantiophylla*. Radial wood section with a druse crystal in a ray cell, × 330; 26, *the same*. The same druse crystal as in FIGURE 25, under polarized light, × 330.

the pits having a circular to elongate outline; some species also had pit arrangements and shapes not easily described; FIGURES 23 and 24, used to illustrate these different patterns, for which the term "variable" will be used here and wherever such arrangements occur in other genera.

Celtis cinnamomea, *C. laevigata* var. *smallii*, and *C. lindheimeri* with some opposite arrangement in addition to alternate; *Celtis pacifica* and *C. ritiensis* with mostly transitional to opposite arrangements; total range in pit diameters for vessel-ray parenchyma pitting and vessel-axial parenchyma pitting is 1.5 to 7 μ.

Axial parenchyma is vasicentric, aliform, and confluent; most species also with terminal parenchyma; *Celtis pumila* with diffuse in addition to vasicentric parenchyma; *Celtis iguanaea*, *C. occidentalis*, *C. pacifica*, *C. paniculata*, *C. paniculata* var. *multiseriata*, *C. pumila*, *C. swartzii*, *C. trinervia*, and *C. ugandensis* with banded parenchyma in addition to the paratracheal types.

Spiral thickenings occur on small vessel elements of all ring porous species; prismatic crystals found in ray and axial parenchyma of all species except *C. adolphi-friderici* and *C. ugandensis*.

Pteroceltis (1, 2). Wood diffuse porous; pore distribution 75 percent solitary, 24 percent radial multiples of 2 to 5 cells and 1 percent clusters of 3 to 4 cells; average pore diameter is 55 μ with a total range of 27 to 90 μ; vessel element wall thickness ranging from 2.5 to 5 μ; perforations simple; end wall angles ranging from 19 to 90°; intervascular pitting crowded, range of pit diameters from 1.5 to 3 μ; average vessel element length 250 μ with a total range of 75 to 390 μ; fiber wall thickness ranging from 2 to 4.5 μ; average fiber length 870 μ with a total range of 510 to 1260 μ.

Uniseriate vascular rays homocellular (Celtis type), biseriate and multiseriate rays heterocellular; height of unicellular rays 2 to 12 cells and 85 to 390 μ; biseriate and multiseriate rays ranging in height from 4 to 41 cells and 75 to 760 μ; width varying from 2 to 5 cells and 10 to 45 μ; dark staining deposits and prismatic crystals in some ray cells; cells containing crystals usually enlarged.

Axial parenchyma vasicentric and confluent; vessel-ray and vessel-axial parenchyma alternate, pits ranging in diameter from 1.5 to 3 μ; prismatic crystals in some axial parenchyma cells.

Ampelocera (4, 5). Wood diffuse porous; pore distribution is 74 to 90 percent solitary, 9 to 22 percent radial multiples of 2 to 5 cells, and 0 to 5 percent clusters of 3 to 4 cells; average pore diameters ranging from 73 to 124 μ with a total range of 30 to 170 μ; vessel wall thickness 3 to 5.5 μ; perforations simple; end wall angles ranging from 30 to 90°; intervascular pit diameters from 6 to 10.5 μ; average vessel element length ranging from 222 to 277 μ with a total range from 148 to 370 μ.

Some fibers septate; fiber wall thickness ranging from 3 to 4.5 μ;

average fiber length ranging from 1088 to 1310 μ with a total range from 888 to 1554 μ.

Uniseriate, biseriate, and multiseriate rays are homocellular, comprised of procumbent cells; uniseriate rays not abundant, ranging in height from 2 to 13 cells and 50 to 225 μ; biseriate and multiseriate rays ranging in height from 5 to 50 cells and 80 to 810 μ; width ranging from 2 to 5 cells and 10 to 40 μ; prismatic crystals occurring in some ray cells.

Axial parenchyma banded in *A. cubensis*, diffuse in *A. edentula*, and terminal in *A. edentula* and *A. glabra*; all species have vasicentric, aliform, and confluent parenchyma; vessel-ray and vessel-axial parenchyma pitting is alternate, the pit diameters ranging from 2.5 to 5 μ.

Zelkova (3, 4). Wood ring porous; pore distribution is 26 to 38 percent solitary, 53 to 73 percent clusters of 3 to 25 cells, and 0 to 8 percent radial multiples of 2 to 3 cells; average pore diameters in the first formed portion of the growth ring ranging from 73 to 150 μ with a total range from 15 to 55 μ; average pore diameter for the last formed part of the growth ring ranging from 23 to 41 μ with a total range of 15 to 55 μ; vessel wall thickness ranging from 1.5 to 5 μ; perforations scalariform (1 bar), simple with vestigial bars, and simple; end wall angles varying from 15 to 90°; intervascular pit diameters ranging from 5 to 9 μ; average vessel element length from 185 to 207 μ with a total range from 111 to 259 μ; tyloses found in *Zelkova serrata* and *Z. sinica*; spiral thickenings found in small vessel elements; storying of vessels in *Z. keakii* and *Z. serrata*.

Imperforate tracheary elements include vascular tracheids and fibers with bordered pits. Some fiber-tracheids are septate in *Z. keakii* and *Z. serrata*; fiber-tracheid wall thickness varying from 2 to 3.5 μ. Average fiber-tracheid length ranges from 1024 to 1687 μ with a total range from 888 to 1998 μ.

Uniseriate rays homocellular (Celtis type), not abundant; biseriate and multiseriate rays mostly homocellular with procumbent cells in *Z. keakii* and *Z. serrata*; but both homocellular and heterocellular in *Z. sinica*; homocellular uniseriate rays ranging in height from 2 to 11 cells and 60 to 260 μ; biseriate and multiseriate rays ranging in height from 6 to 90 cells and 110 to 1165 μ, in width from 2 to 10 cells and 10 to 115 μ; prismatic crystals and dark contents found in some ray cells; some crystal containing cells enlarged.

Axial parenchyma vasicentric; vessel-ray and vessel-axial parenchyma pitting alternate with pit diameters from 2.5 to 5 μ; prismatic crystals and dark deposits occurring in some cells; crystalliferous strands found in *Z. keakii*.

Hemiptelea (1, 2). Wood ring porous; pore distribution 42 percent solitary, 50 percent clusters of 3 to 15 cells, and 8 percent radial multiples of 2 to 5 cells; average pore diameter for the early part of the growth ring 70 μ with a range from 15 to 165 μ; average for the last formed portion of the ring is 22 μ with a range from 10 to 30 μ; perforations scalariform

(1–2 bars), simple with vestigial bars, and simple; end wall angles varying from 14 to 90°; intervascular pits ranging in diameter from 3.5 to 6.5 μ; average vessel element length 220 μ with a range of 148 to 296 μ; small vessel elements with spiral thickenings; some storying of vessels occurring.

Imperforate tracheary elements include vascular tracheids and fibers; some fibers septate; vascular tracheids with spirals; fiber wall thickness ranging from 2 to 5 μ; average fiber length 1100 μ with a range from 888 to 1332 μ.

Uniseriate rays homocellular (Celtis type) with procumbent cells; ranging in height from 3 to 12 cells and 70 to 300 μ; biseriate and multiseriate rays heterocellular; height ranging from 6 to 45 cells and 95 to 675 μ, width ranging from 2 to 28 cells and 25 to 280 μ; prismatic crystals and dark staining materials found in some ray cells.

Axial parenchyma vasicentric and terminal; vessel-ray and vessel-axial parenchyma pitting alternate with pit diameters from 1.5 to 2.5 μ.

Trema (9, 11). Wood diffuse porous; pore distribution 53 to 88 percent solitary, 6 to 42 percent radial multiples of 2 to 4 cells, and 0 to 6 percent clusters of 3 to 6 cells; pore diameter averaging from 80 to 117 μ with a total range of 15 to 165 μ; perforations simple; end wall angles varying from 10 to 90°; intervascular pitting crowded in *Trema guineënse*, *T. micrantha*, and *T. vieillardii*; pit diameters ranging from 2.5 to 6.5 μ; average vessel element lengths ranging from 281 to 566 μ with a total range from 185 to 832 μ; vessels in *T. guineënse*, *T. lamarckiana*, and *T. micrantha* with tyloses; *Trema bracteolata* with septate fibers; fiber wall thickness ranging from 1 to 5 μ; average fiber lengths ranging from 777 to 1295 μ with a total range from 518 to 1702 μ.

Uniseriate rays homocellular (Celtis type), ranging in height from 2 to 21 cells and 55 to 785 μ; biseriate and multiseriate rays heterocellular, ranging in height from 4 to 7 cells and 100 to 1875 μ and in width from 2 to 7 cells and 10 to 60 μ; dark staining material occurring in many ray cells; prismatic crystals found in ray cells of *Trema vieillardii*.

Axial parenchyma vasicentric; vessel-ray and vessel-axial parenchyma pitting "variable" to alternate; pit diameters ranging from 2.5 to 6.5 μ.

Parasponia (1). Wood diffuse porous; pore distribution 77 percent solitary, 20 percent radial multiples of 2 to 3 cells, and 3 percent clusters of 3 cells; average pore diameter 143 μ with a range from 95 to 225 μ; vessel element walls ranging in thickness from 2 to 3.5 μ; perforations simple; end wall angles varying from 16 to 90°; intervascular pitting crowded with a range of pit diameters 6 to 9 μ; average vessel element length is 381 μ with a range from 240 to 450 μ; fiber thickness varying from 2 to 3 μ; average fiber length 890 μ with a range from 456 to 1110 μ.

Uniseriate rays homocellular, comprised of procumbent cells and ranging in height from 2 to 13 cells and 75 to 390 μ; biseriate and multiseriate rays heterocellular, ranging in height from 5 to 38 cells and 160 to 860 μ, in width from 2 to 4 cells and 20 to 75 μ; dark staining deposits and prismatic crystals found in some ray cells.

Axial parenchyma vasicentric and terminal; dark staining deposits and prismatic crystals found in some cells; vessel-ray and vessel-axial parenchyma pitting alternate with a pit diameter range from 5 to 7.5 μ.

Aphananthe (2). Wood diffuse porous; pore distribution 66 percent solitary, 30 percent radial multiples of 2 to 4 cells, and 4 percent clusters of 3 to 5 cells; average pore diameter 85 μ with a total range of 50 to 150 μ; vessel wall thickness ranging from 2.5 to 5.5 μ; perforations simple; end wall angles of vessel elements ranging from 15 to 90°; intervascular pit diameters ranging from 3.5 to 6.5 μ; average vessel element length 290 μ with a total range from 222 to 518 μ; tyloses found in vessels of *A. philippinensis*; fiber wall thickness ranging from 2.5 to 4.5 μ; average fiber length 1190 μ with a total range from 1036 to 1443 μ.

Uniseriate rays homocellular (Celtis type) comprised of procumbent cells ranging in height from 3 to 10 cells and 65 to 235 μ; biseriate and multiseriate rays heterocellular, ranging in height from 3 to 43 cells and 65 to 525 μ, in width 2 to 5 cells and 10 to 40 μ; dark staining deposits found in some ray cells.

Axial parenchyma is vasicentric, confluent, and terminal; *Aphananthe philippinensis* also exhibits some banding; vessel-ray and vessel-axial parenchyma pitting alternate to "variable," pit diameters ranging from 2.5 to 6.5 μ.

Mirandaceltis (1). Wood diffuse porous; pore distribution 73 percent solitary, 20 percent radial multiples of 2 to 3 cells, and 7 percent clusters of 3 to 6 cells; average pore diameter 57 μ with a range from 35 to 85 μ; vessel wall thickness 2.5 to 5 μ; perforations simple; end wall angles ranging from 35 to 90°; intervascular pitting crowded with a pit diameter from 3 to 4 μ; average vessel element length 307 μ, ranging from 148 to 407 μ; tyloses present in vessels.

Fiber wall thickness 2 to 3 μ; average fiber length 828 μ with a range from 740 to 962 μ.

Uniseriate rays homocellular (Celtis type), ranging in height from 2 to 15 cells and 65 to 275 μ; biseriate and multiseriate rays heterocellular, ranging in height from 6 to 30 cells and 100 to 510 μ, in width from 2 to 4 cells and 25 to 40 μ; some ray cells with prismatic crystals and dark staining deposits.

Axial parenchyma is vasicentric, confluent, and terminal; prismatic crystals and dark staining contents found in some cells; vessel-ray and vessel-axial parenchyma pitting alternate to "variable"; pits ranging in diameter from 2.5 to 5 μ.

Gironniera (5, 9). Wood diffuse porous; pore distribution from 51 to 92 percent solitary, 6 to 46 percent radial multiples of 2 to 7 cells, and

0 to 6 percent clusters of 3 to 8 cells; pore diameters ranging from 88 to 186 μ with a total range from 40 to 255 μ; vessel wall thickness ranging from 2.5 to 5 μ; perforations simple; end wall angles varying from 30 to 90°; intervascular pit diameters ranging from 2.5 to 12.5 μ; average vessel element lengths ranging from 333 to 407 μ with a total range of 148 to 1147 μ; tyloses present in *Gironniera celtidifolia*.

Some fibers septate in *Gironniera celtidifolia*; fiber wall thickness varying from 1.5 to 6.5 μ; average fiber length ranging from 1188 to 1795 μ with a total range from 814 to 2590 μ.

Uniseriate rays homocellular (Celtis type); uniseriate rays of *Gironniera cuspidata* and *G. nitida* ranging in height from 2 to 13 cells and 60 to 275 μ; biseriate and multiseriate rays ranging in height from 5 to 62 cells and 85 to 1115 μ and in width from 2 to 5 cells and 15 to 45 μ; uniseriate rays of *G. celtidifolia*, *G. nervosa*, and *G. subaequalis* ranging in height from 2 to 18 cells and 90 to 1335 μ; biseriate and multiseriate rays ranging in height from 5 to 89 cells and 230 to 2475 μ, in width from 2 to 14 cells and 20 to 205 μ; prismatic crystals present in ray cells of *G. cuspidata* and *G. nitida*.

Axial parenchyma vasicentric in *G. nervosa*; vasicentric, confluent, and banded in *Gironniera celtidifolia*, *G. cuspidata*, and *G. nitida*; vasicentric, aliform, and confluent in *G. subaequalis*; prismatic crystals present in some cells of *G. cuspidata* and *G. nitida*; dark deposits present in some ray and axial parenchyma cells; vessel-ray and vessel-axial parenchyma pitting are "variable" to alternate; pit diameters ranging from 2.5 to 10 μ.

Chaetachme (2). Wood diffuse porous; pore distribution 60 percent solitary, 34 percent radial multiples of 2 to 8 cells, and 6 percent clusters of 3 to 7 cells; average pore diameter 78 μ with a range of 35 to 135 μ; vessel wall thickness from 1.5 to 6.5 μ; perforations simple; vessel end wall angles varying from 15 to 90°; intervascular pit diameters from 3.5 to 6.5 μ; average vessel element length 450 μ with a range of 296 to 666 μ; tyloses present in *C. aristata*.

Fibers septate; wall thickness from 1.5 to 5.5 μ; average fiber length 1540 μ with a total range from 1184 to 2146 μ; uniseriate rays homocellular (Celtis type), ranging in height from 2 to 10 cells and 50 to 235 μ; biseriate and multiseriate rays heterocellular, ranging in height from 7 to 96 cells and 65 to 1920 μ, in width from 2 to 5 cells and 20 to 35 μ; dark staining deposits in ray cells of *C. microcarpa*.

Axial parenchyma vasicentric, confluent, and banded; vessel-ray and vessel-axial parenchyma pitting "variable" to alternate; pit diameters from 2.5 to 6.5 μ.

Lozanella (1). Wood diffuse porous; pore distribution 72 percent solitary, 28 percent radial multiples of 2 to 4 cells; average pore diameter 140 μ, ranging from 60 to 200 μ; vessel wall thickness 2 to 3 μ; perforations simple; end wall angles from 36 to 90°; intervascular pit diameters from 7 to 9 μ; average vessel length 468 μ, ranging from 300 to 630 μ; tyloses present.

Some fibers septate; wall thickness from 3.5 to 5 μ; average fiber length 930 μ with a range from 630 to 1350 μ.

Uniseriate rays homocellular (Celtis type) comprised of procumbent cells, range in height from 2 to 10 cells and 125 to 510 μ; biseriate and multiseriate rays heterocellular, ranging in height from 7 to 91 cells and 200 to 2500 μ, in width from 2 to 7 cells and 40 to 85 μ; druses and dark staining contents present in some ray cells (FIGURES 25, 26).

Axial parenchyma vasicentric, confluent, and banded; some cells with druses; vessel-ray and vessel-axial parenchyma pitting "variable" to alternate; pit diameters from 3.5 to 6.5 μ.

DISCUSSION

The validity of using secondary xylem characters for systematic purposes has been established through the studies of Bailey and Tupper (1918), Frost (1930a, 1930b, 1931), Chalk and Chattaway (1935), Kribs (1935, 1937), Barghoorn (1940, 1941a, 1941b), and many others. Following these basic investigations, application of concepts has provided valuable information on the relationships of many disputed taxa, e.g., Tippo (1938), Heimsch (1942), Stern (1952), and Carlquist (1960). The techniques of systematic wood anatomy and its application to problems in plant phylogeny was summarized by Tippo (1946). Bailey, in 1957, wrote: "The chief trends of evolutionary specialization in the cambium and xylem of dicotyledons are now so reliably established (except in the case of certain patterns of wood parenchyma distribution) that they can be utilized to advantage in studying salient problems of phylogeny and classification." Use of leaf anatomical characters for systematic problems was summarized by Carlquist (1961), who noted, "The leaf is perhaps anatomically the most varied organ of angiosperms, and its anatomical variations often occur closely with generic and specific — occasionally — familial lines."

In any comparative systematic study using only anatomical features would invite misconceptions. Anatomical characters are most useful when employed in conjunction with data from other fields of botanical endeavor. Important correlative data might come from fields of phytochemistry, cytotaxonomy, paleobotany, embryology, morphogenesis, phytogeography, etc. It is important to consider and evaluate studies from these investigative fields and to apply pertinent findings to those from plant anatomy. Consequently, a complex of characters must be examined in an attempt to avoid mistaking convergent evolution for valid genotypic similarities which have resulted from derivation of taxa from common ancestry.

ANATOMY

The anatomical observations made in this study are in basic agreement with previous works. Scalariform perforations are reported here for the first time in the secondary xylem of some species of *Celtis*, *Hemiptelea*, *Planera*, *Ulmus*, and *Zelkova*.

The Ulmaceae as a family are diverse anatomically. However, there are many anatomical characters of leaf and wood which pervade the entire group. Among the common features in leaves are the anomocytic stomatal apparatus, bulbous-based unicellular trichomes, similar multicellular hairs, parenchymatous bundle sheaths and extensions, presence of silica, calcium carbonate, and mucilage, and all venation patterns basically pinnate. Common features of the xylem include relatively short vessel elements (less than 350 μ long); alternate intervascular pitting; mostly simple perforations; relatively short fibers (less than 900 μ long); simple to slightly bordered fiber pits; uniseriate, biseriate, and multiseriate vascular rays; and some homocellular vascular rays in all genera.

The two tribes can be separated to a greater or lesser extent on the following anatomical grounds:

ULMEAE	CELTEAE
LEAF	
"Simply" craspedodromous venation pattern	Brochidodromous venation pattern
Pegged cystoliths absent	Pegged cystoliths present
WOOD	
Rays homocellular only	Rays homocellular and heterocellular
Vessel-ray and vessel-axial parenchyma pitting alternate	Vessel-ray and vessel-axial parenchyma pitting "variable" to alternate

The ulmaceous genera are more or less distinct anatomically. *Celtis* can be divided into two groups on the basis of ring *versus* diffuse porosity. The ring porous species are similar to *Ulmus* (which is all ring porous) in pore distribution, presence of spirals in small vessel elements, and types of perforation plates (scalariform, simple with vestigial bars, and simple). However, *Celtis* is easily distinguishable by the presence of heterocellular biseriate and multiseriate rays in the secondary xylem, by the brochidodromous venation pattern in the leaf, by the presence of pegged cystoliths and of the compact spongy mesophyll. *Ulmus* is distinguishable from ring porous species of *Celtis* (and from the diffuse porous species as well) in wood anatomy by homocellular biseriate and multiseriate rays and crystalliferous strands, and in leaf anatomy by the "simply" craspedodromous venation pattern in the leaf, loose spongy mesophyll, and lack of pegged cystoliths.

On the basis of floral morphology and geographical distribution *Celtis* was divided into the subgenera CELTIS, SPONIOCELTIS, SOLENOSTIGMA, and MOMISIA and *Ulmus* into the subgenera OREOPTELEA, DRYOPTELEA, and MICROPTELEA by Planchon (1873). On the basis of external morphology, Rehder (1940) divided *Ulmus* into the sections BLEPHAROCARPUS, CHAETOPTELEA, ULMUS (§ *Madocarpus*), MICROPTELEA, and TRICHOPTELEA. Anatomical evidence neither sustains nor rejects any of these groupings.

In the other Ulmeae, *Phyllostylon* and *Holoptelea* both have cystoliths in the leaves as well as many other leaf characters in common. However, they can be separated on the basis of wood anatomy: *Holoptelea* has only few uniseriate rays, biseriate and multiseriate rays are storied, and ray cells lack crystals; *Phyllostylon* has many uniseriate rays, rays are not storied, and prismatic crystals occur in ray cells. *Planera* is distinguished from *Holoptelea* and *Phyllostylon* by the "simply" craspedodromous venation pattern in the leaf, whereas, *Holoptelea* and *Phyllostylon* show a brochidodromous pattern. In wood anatomy *Planera* is distinguished from *Holoptelea* and *Phyllostylon* by the pore distribution: *Planera* has mostly solitary pores and clusters, *Holoptelea* and *Phyllostylon* have mostly solitary pores and radial multiples. *Planera* has many xylem anatomical features in common with *Ulmus*. However, *Planera* has spiral thickenings in all vessel elements and *Ulmus* only has spirals in small vessel elements.

An apparent anomaly occurs among the studied specimens of *Planera aquatica*, two of these are diffuse porous and the third is ring porous. However, all *Planera* specimens have the characteristic pore distribution of ulmaceous ring porous species (solitary pores and clustered pores highest in percent with radial multiples least in percent). It should also be noted that in the ring porous specimen the difference in pore diameter in the first formed portion of the ring is only nine microns greater than the pore diameters in the last formed portion of the ring. In other ring porous species of the Ulmaceae the first formed pores are two to six times the diameter of the last formed pores. Apparently, *Planera* has the genetic capability of being either diffuse or ring porous. The less pronounced ring porosity in *Planera* is probably the result of the more equable climate of its habitat in the southeastern United States.

Chaetoptelea has many anatomical features in common with *Ulmus*, but the two genera differ in the following points: *Chaetoptelea* has mostly solitary and radial pore multiples, whereas, all *Ulmus* species have mostly solitary and clustered pores; *Chaetoptelea* lacks spiral thickenings in all vessel elements, while all *Ulmus* species have spirals in small vessels. Record and Hess (1943) report spirals in the "smallest vessels of *Chaetoptelea*"; however, none was observed in this study.

In the Celteae, *Celtis* is such a large and diverse genus that anatomically it is difficult to distinguish it from *Pteroceltis*, *Mirandaceltis*, *Gironniera*, and *Chaetachme*. *Ampelocera* is similar to *Celtis* in leaf anatomy, but distinct on the basis of wood anatomy as *Ampelocera* has septate fibers and all homocellular rays while *Celtis* lacks septate fibers and has heterocellular rays. *Zelkova* is distinct because of its "simply" craspedodromous leaf venation pattern, lack of pegged cystoliths, and mostly homocellular rays. *Hemiptelea* is separated from both these genera by the "simply" craspedodromous leaf venation pattern, presence of pegged cystoliths, and storying of vessels. *Trema* has the acrodromous leaf venation pattern, uneven leaf epidermis, and septate fibers in the xylem. *Parasponia* and *Aphananthe* both have a "simply" craspedodromous leaf venation pattern, but in other anatomical features are quite similar to *Celtis*. *Lozanella* is similar to *Celtis* in all respects except that it has druses in the vascular ray cells. It was not possible in either Celteae or Ulmeae to separate most species within a genus on the basis of wood and leaf anatomy.

PROBLEM GENERA

The question whether *Chaetoptelea* should be a separate genus or part of *Ulmus* cannot be answered on the basis of a few characters. Dr. Leo Hickey of the Smithsonian Institution (personal communication) is able to distinguish fossil *Chaetoptelea* leaves from fossil *Ulmus* leaves on the basis of venation. Standley (1922) stated that "All the species of the latter genus [*Ulmus*], however, have a broadly winged fruit, while in *Chaetoptelea* there is no vestige of a wing, and this probably is a sufficient basis for the maintenance of Liebmann's genus." Leaf anatomy of *Chaetoptelea mexicana* is quite similar to *Ulmus*. In wood anatomy both genera are ring porous, but two distinct differences in the secondary xylem occur: *Chaetoptelea* has mostly solitary and radial pore multiples, whereas, all *Ulmus* species have mostly solitary and clustered pores; *Chaetoptelea* lacks spiral thickenings in vessel elements while all *Ulmus* species have spiral wall thickenings in small vessel elements. Metcalfe and Chalk (1950) state, "The most valuable taxonomic vessel characters are the distribution and pattern of the pores as seen in transverse sections." Thus, it would appear that *Chaetoptelea* as a separate genus may be supported by wood anatomy.

Sharp (1958) created a separate genus, *Mirandaceltis*, for the single species *Celtis monoica* Hemsl. on the following basis: "This genus differs from *Celtis* in the venation of the leaves which resembles that of *Ulmus* . . . The drupaceous fruit is also larger and less spherical than that usually found on *Celtis* . . ." Some differences in leaf anatomy were noted in that some unicellular hairs are barbed in *Mirandaceltis* and not in *Celtis*; cystoliths are of the pegless variety in *Mirandaceltis*, whereas, all *Celtis* species, except *C. schippii*, have pegged cystoliths. It must be stated, however, that the overall venation pattern of *Mirandaceltis* is similar to that in most *Celtis* species (brochidodromous), whereas, in *Ulmus* the venation pattern is "simply" craspedodromous. I find no difficulty in distinguishing the pattern of venation in *Mirandaceltis* from that in *Ulmus*, including the leaf specimens of *Mirandaceltis* illustrated in Sharp (1958). On the basis of wood anatomy *Mirandaceltis* cannot be separated from *Celtis*. The taxonomic status of this genus is questionable and anatomically it seems to be only a minor variant of *Celtis*. However, further study should be undertaken to determine the possible taxonomic importance of the pegged versus unpegged cystoliths.

The genus *Gironniera* contains two subgenera, GIRONNIERA (*Nematostigma* Planch.)[2] with *G. celtidifolia*, *G. nervosa*, and *G. subaequalis* and

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[2] According to ICBN, Art. 22, 1966, the name GIRONNIERA must be used for the subgenus containing the type species.

GALUMPITA Blume with *G. cuspidata*, *G. nitida*, and *G. reticulata* (Bentham & Hooker, 1862; Engler & Prantl, 1893). Anatomically the two subgenera are most readily separated by the much larger secondary xylem rays of the former group. Subg. GALUMPITA is reported to have possible affinities with *Chaetachme* (Record, as a footnote to Janssonius, 1932). On the basis of wood and leaf anatomy there are no features which would negate a relationship between subg. GALUMPITA and *Chaetachme*. On the basis of leaf anatomy it is unlikely that subg. GIRONNIERA is related to *Trema*, however, since there are several differences: overall venation pattern is acrodromous in *Trema* and brochidodromous in subg. GIRONNIERA, pegged cystoliths are lacking in subg. GIRONNIERA but present in *Trema*, and the occurrence of a multiple epidermis in *Trema*, absent in *Gironniera* subg. GIRONNIERA. *Trema* and subg. GIRONNIERA are similar in overall wood anatomy.

Subgenus GIRONNIERA is similar to *Parasponia* in wood anatomy, but differs in leaf anatomy, *Parasponia* having neither pegged cystoliths nor barbed hairs, subg. GIRONNIERA having both. Further detailed study of the wood and leaf anatomy is necessary to determine species variation before this problem can be solved.

FAMILY RELATIONSHIPS

The question has been raised whether Ulmaceae should be one family with two subgroups or two separate families. Link (1831) proposed two families, Ulmaceae and Celtaceae (as Celtidaceae). Grudzinskaya (1967) supported this contention and suggested that the Celteae (as Celtideae) has more characters in common with the Moraceae than with the Ulmeae, but not enough to incorporate it into the Moraceae. Grudzinskaya further suggests transferring *Hemiptelea* and *Zelkova* from Celteae to Ulmeae. It should be mentioned that her conclusions were drawn without prior study of the secondary xylem of the Ulmaceae.

The recommendation to split this family in two fails to account for genera with transitional characters in each tribe, e.g., *Ampelocera*, *Phyllostylon*, *Zelkova*, *Planera*, and *Hemiptelea*. Baillon (1880) stated that the "Celtideae, on the one hand, could not be disjoined from the Elms, the fruit of *Planera* being intermediate between the drupes of *Celtis* and the samarae of Ulmus." Lindley (1853) stressed that the Celteae (Celtideae) and Ulmeae should be considered "mere forms of one type." The maintenance of two subgroups within the Ulmaceae has, accordingly, been followed by most taxonomists.

Wood and leaf anatomy shed additional light on this problem by illustrating further transitional characters. *Phyllostylon* has homocellular rays, a character of the Ulmeae, and pegged cystoliths, a character of the Celteae; *Zelkova* has many secondary xylem characters in common with both groups: the venation pattern is like the Ulmeae and the biseriate and multiseriate wood rays are heterocellular (a character of the Celteae) and homocellular (as in Ulmeae). *Hemiptelea* is like *Zelkova* in many respects and in addition it has pegged cystoliths (as in Celteae). *Ampelocera*, which is placed in, and is like the Celteae in most leaf and wood characteristics, has homocellular biseriate and multiseriate rays (a character of Ulmeae). Even when the secondary rays are considered in other Celteae, the homocellular type is not totally absent since it was noted that homocellular types of transitional nature are found. In the Anatomy portion of the DISCUSSION of this paper is a complete listing of anatomical features held in common by Ulmeae and Celteae.

As far as relating the Ulmaceae to the Moraceae is concerned, most present day systematists acknowledge the naturalness of the Urticales, among them Cronquist (1968), Hutchinson (1969), Taktahjan (1969). A notable exception is Thorne (1963) who thinks that the Urticales in the sense of the taxonomists noted above, particularly of Cronquist, comprise convergent groups. Nair and Sharma (1965), on the basis of pollen studies, state that the Urticales are a homogeneous group. If Urticales is composed of genetically closely related elements, as is conceded by most authorities today, it would not be at all irregular for genera in related families to possess certain common characteristics. That is exactly what occurs between the Moraceae and some members of the Celteae. From the point of view of many morphological and anatomical features, Ulmaceae should be considered a natural taxon with two, more or less distinct subgroups having transitional forms.

When a comparison is made between the relatively small family, Ulmaceae, and the relatively large family, Moraceae (53 genera and 1,400 species), statistical probability of similarities through parallel evolution is very high. The dangers of comparing a small taxon with a large family have been pointed out by Stern and Brizicky (1958).

The separation of the two subgroups within the Ulmaceae into two separate families is not supported by leaf and secondary xylem anatomy. Other features also suggest a cohesiveness within Ulmaceae; the nodal anatomy, for example, is trilacunar throughout the family (Sinnott & Bailey, 1914); the haploid chromosome number of 14 is reported in all genera investigated to date; sieve tube elements are short with slightly oblique to transverse simple sieve plates (Zahur, 1959); and Lebreton (1965), on the basis of flavonoid analysis, supported the distinctness of the Ulmaceae from other families in the Urticales.

GENERAL ANATOMICAL CONSIDERATIONS

The use of the terms loose and compact in relation to the spongy mesophyll and the possible taxonomic significance of the mesophyll has not been reported before. In general, *Ulmus* is characterized by a loose spongy mesophyll and *Celtis* by a compact spongy mesophyll. All leaf specimens were selected at random. Thus, it would appear that any variation resulting from the selection of "sun" versus "shade" leaves would also have been random throughout each genus. Consequently, this variation in leaf mesophyll noted for *Ulmus* and *Celtis* is probably genetic and not related to environment. However, the use of this character for taxonomic purposes is too uncertain at present and further intensive study is required to establish its value.

Cystoliths were classified as pegged and unpegged. It is obvious from the descriptions of the two that they differ in composition and structure. Pegged cystoliths have a cellulose peg upon which calcium carbonate and silica are deposited, whereas unpegged cystoliths are deposited without a peg and appear to be composed mainly of silica. The taxonomic significance of the presence and distribution of pegged and unpegged cystoliths, as well as of mineral placks, crystals, and mucilage is not clear. All members of Ulmaceae secrete and deposit silica, calcium carbonate, calcium oxalate, and mucilage in varying degrees. The major differences are in the position and form of the deposits. Further study of the secretions and deposits in the leaf and wood of the Ulmaceae is needed. The overall venation pattern and presence or absence of bundle sheaths on terminal tracheary elements seems to be constant within a genus; however, the effects of environment and species variation are not known. The use of such characters in taxonomic treatments may prove valuable later.

One difficulty arising from the investigation of any family which has both ring and diffuse porous species growing in both temperate and tropical regions, is the need for caution in interpreting comparative data between the two groups. Gilbert (1940) has suggested that the ring porous condition is a response to a temperate (seasonal) environment and that resulting evolution has given impetus to development of other so-called "advanced" characters, such as spirals in vessel elements. Others have addressed themselves to this problem and have arrived at basically the same conclusion (Tippo, 1938; Metcalfe & Chalk, 1950). The present study tends to support this contention. Although ring porous species of *Celtis*, *Zelkova*, *Hemiptelea*, and *Ulmus* possess certain associated characters, such as spirals in the vessel elements and relatively shorter fibers and vessels which appear to make them advanced anatomically, they also have scalariform perforation plates and simple plates with vestigial bars, both considered to be primitive features. Diffuse porous species of Ulmaceae and other woody Urticales invariably have simple perforation plates, exclusively. Thus, ring porous species, although possessing some associated advanced characters also have retained certain primitive ones.

Cox (1941) demonstrated in *Celtis* that species of tropical regions are diffuse porous and lack spirals in the vessels while species of temperate areas are ring porous and have spirals in the vessels. *Celtis* species from the present study show the same pattern. In the specimens of *Planera aquatica* examined, two were diffuse porous and one was ring porous. The ring porous specimen was not as markedly ring porous (see "Results" and "Anatomy" portion of "Discussion") as the material of ring porous species of other ulmaceous genera. This condition is probably related to the less pronounced seasonal environment in which *P. aquatica* grows in the southeastern United States. I investigated species of *Quercus* (Fagaceae), which also have ring and diffuse porous members, to determine if there is any correlation in this genus between porosity and seasonality due to geographical location. Wood specimens of *Quercus* from the Smithsonian Institution wood collection and *Q. virginiana* from Key Largo, Florida, collected by William L. Stern were checked for porosity by means of a hand magnifier. As can be seen from TABLE 5 the temperate zone species are all ring porous. However, the tropical and subtropical species are diffuse porous or weakly ring porous. *Quercus virginiana*, like *Planera aquatica*, exhibits both ring and diffuse wood porosity. The only apparent difference in the expression of the porosity appears to depend on the degree of seasonality. The abruptness of seasonal change may be more significant than latitudinal position. *Quercus* species from the latitudinal tropics often inhabit submontane and montane positions where the climate is actually quite cool. The significance of these positions, as far as plant growth is concerned, is the lack of sharp seasonality which does characterize habitats in true temperate zones. For example, in some *Quercus* species from the latitudinal tropics, growth rings themselves are vague, in sharp contrast to their formation in the true temperate zone inhabited by other species of *Quercus*. It appears then, that the genetic potential for the production of ring porous wood occurs in certain species, such as *Planera aquatica* and *Quercus virginiana*, but its expression depends on a seasonal environment.

TABLE 5. **Wood porosity of Quercus species arranged in a north-south geographical axis**

SPECIES	R–RING POROUS D–DIFFUSE POROUS	COLLECTION SITE
QUERCUS		
coccinea Muenchh.	R	Brooklyn, N.Y.
alba L.	R	Philadelphia, Pa.
laurifolia Michx.	R	Dismal Swamp, Va.
phellos L.	R	Dismal Swamp, Va.
falcata Michx.	R	Gainesville, Fla.
virginiana Mill.	R	Del Rio, Texas
virginiana	D	Key Largo, Fla.
candicans Née	R–D	Huehuetenango, Guatemala (6,000 ft.)
oleoides Mull.	D	Augustine, British Honduras (2,000 ft.)
copeyensis Mull.	D	Cartago, Costa Rica (8,000 ft.)
baruensis Mull.	R–D	Cerro de Punta, Panama (6,000 ft.)

The solution of the problem of evaluating and comparing characters probably evolved in response to different environmental conditions, tropical *versus* temperate, involves careful evaluation of all characters with conclusions based on study of as much of the phenotype as possible. Also, within species, even though certain characters appear to be correlated with environment (ring porosity and spirals in temperate regions), other characters remain unaffected and constant and tend to show the relationship between the tropical and temperate elements of these taxa. *Celtis* exemplifies this since it includes species showing ring and diffuse porous wood but having many other anatomical characters in common, such as brochidodromous venation pattern, tight spongy mesophyll, cystoliths in leaves, and heterocellular with transitions to homocellular rays in the secondary xylem. The Ulmaceae as a whole is a good example of this structural-environmental phenomenon in that, even though there are species of temperate and tropical zones (ring porous and diffuse porous), many anatomical characters are held in common by both groups. Consequently, ring porosity and spirals in vessels should not be considered as an advanced anatomical condition in comparisons between taxa of temperate and tropical regions. Instead, ring porosity and spirals should be considered as specializations in Ulmaceae which are correlated with a seasonal temperate environment.

ORDINAL PLACEMENT AND PHYLOGENETIC CONSIDERATIONS

Cronquist, Hutchinson, and Taktahjan all agree that the Urticales should be assigned to a larger category related to and including the Hamamelidales. The only modern phylogenist to disagree is Thorne who places the Urticales in a group having as its progenitor the Malvales. On purely morphological grounds, it is difficult to justify placing the Urticales in a group which has anything but reduced anemophilous flowers; the Malvales complex does not have reduced flowers; the Hamamelidales complex does. TABLE 6 summarizes some external morphological features of both groups. Looking at wood anatomy to help resolve this problem, it is appropriate to quote Bailey (1957): "Thus far, the evolutionary trends in the cambium and xylem of dicotyledons, when considered by themselves, have been most reliable and significant in negations." If we consider the two largest orders on either side of the Urticales (Thorne, Malvales and Rhamnales; Cronquist, Hamamelidales and Juglandales) we find that Urticales are more closely allied in wood anatomy to the latter orders; for example: fibers of Malvaceae and Rhamnaceae have simple pits and perforation plates are exclusively simple, fibers in Hamamelidaceae have distinctly bordered pits and the perforation plates are scalariform, fibers in Juglandaceae have bordered pits and the perforation plates are scalariform to simple (Metcalfe & Chalk, 1950). The urticalean families have fibers with slightly bordered to simple pits and the perforation plates are mostly simple with some scalariform perforation plates in the Ulmaceae. A group with specialized secondary xylem is not likely to give rise to a group with more primitive features. Considering morphological and secondary xylem characters, the systems of Cronquist, Hutchinson, and Takhtajan reflect a more natural placement of the order Urticales.

TABLE 6. **Comparison of morphological features of the largest orders on either side of Urticales**

CRONQUIST (1968)

	HAMAMELIDALES	URTICALES	JUGLANDALES
Growth form	trees-shrubs	trees, shrubs, herbs	trees
Leaf arrangement	alternate	alternate (rarely opposite)	alternate
Calyx parts	4–5	2–8	2–6
Corolla parts	4–5 or absent	absent	absent
Stamens	2–8	2–8	3–40
Carpels	2	1–(2)	2–3
Ovary position	inferior-superior	superior	superior-inferior
Ovules	1 or more	1	2(1)
Ovule position	pendulous	erect-pendulous	erect

THORNE (1968)

	MALVALES	URTICALES	RHAMNALES
Growth form	trees-shrubs	trees-shrubs, herbs	trees, shrubs
Leaf arrangement	alternate	alternate	alternate-opposite
Calyx parts	3–5	2–8	4–5
Corolla parts	3–5	absent	4–5 or absent
Stamens	numerous	2–8	4–5
Carpels	2–10+	1(2)	2–4
Ovary position	superior	superior	superior
Ovules	1–many	1	1–2
Ovule position	pendulous	erect-pendulous	erect-pendulous

Tippo (1938), working with wood anatomy, Bechtel (1921), studying floral morphology, and Lebreton (1965), investigating flavonoids, demonstrated the primitive position of the Ulmaceae within the Urticales. The current anatomical study supports this view.

The Ulmaceae, in respect to all angiosperms, should be considered moderately specialized to specialized in wood anatomy because of the mostly simple perforation plates; short vessel elements; fibers short to medium in length; at least some vessel-end-wall angles of 90°; alternate intervascular pitting; rays homogeneous or with a tendency to homogeneity; storying of vessels, fibers, and rays in some species; and axial parenchyma occurring in groups (apotracheal banded, aliform, confluent). This view is also supported by the specialized condition of the secondary phloem exhibited by sieve tube elements which have slightly oblique to transverse simple sieve plates (Zahur, 1959).

SUMMARY AND CONCLUSIONS

The Ulmaceae is considered to be a natural taxon because of the many leaf and wood characters held in common by its constituent elements. These include the anomocytic stomatal apparatus; bulbous-based unicellular trichomes; similar multicellular hairs; parenchymatous bundle sheaths; presence of silica, calcium carbonate, and mucilage; pinnate venation patterns; relatively short vessel elements, alternate intervascular pitting; mostly simple perforations; relatively short fibers; vascular rays uniseriate, biseriate, and multiseriate, at least some of which are homocellular; and fibers with simple to slightly bordered pits. The tribes of Hutchinson (1967) are more or less distinct anatomically.

This study supports the primitive position of Ulmaceae within the Urticales. Wood anatomy negates the placement of the Urticales near the Malvales and Rhamnales by Thorne (1968) and supports Cronquist (1968) and others in placing the order near the Hamamelidales and Juglandales. In relation to other angiosperm families, Ulmaceae is considered moderately advanced to advanced because of its many specialized wood features, such as simple perforations; short vessel elements; short fibers; vessel-element end-walls of 90°; alternate intervascular pitting; homogeneous rays or a tendency to produce homogeneous rays; storied vessels, fibers, and rays; and apotracheal banded, aliform, and confluent axial parenchyma.

Wood anatomy supports the separation of *Chaetoptelea* from *Ulmus*, as previously noted. *Mirandaceltis*, though differing from *Celtis* in some characters cannot be separated on the basis of wood anatomy.

Gironniera may be divided into two subgenera based on anatomical characters. Subg. GIRONNIERA with large vascular rays and subg. GALUMPITA with smaller vascular rays. Wood and leaf anatomy are insufficient bases on which to separate the subg. GALUMPITA from *Chaetachme*. Subg. GIRONNIERA is reportedly related to *Trema* or *Parasponia*. *Trema* differs in having pegged cystoliths, a multiple epidermis, and acrodromous venation. *Parasponia* differs in leaf anatomy from *Gironniera* in having pegged cystoliths and lacking barbed unicellular hairs. *Trema*, *Parasponia*, and *Gironniera* subg. GIRONNIERA are similar in wood anatomy. Further detailed study of wood and leaf anatomy is warranted to determine variation within species before these *Gironniera* problems can be resolved.

The use of "loose" *versus* "compact" spongy mesophyll and the occurrence and distribution of cystoliths, crystals, mineral placks, and mucilage deserve further study since they might be usefully employed in taxonomic studies. *Ulmus* has a "loose" spongy mesophyll while *Celtis* exhibits a "compact" spongy mesophyll. However, other genera in the Ulmaceae are less consistent. Here too, intensive study on variation within species and effects of environment on production and distribution of mineral deposits and mucilage is needed.

Ring porous woods and associated characters, such as spirals in vessel elements, are considered to be structural modifications correlated with seasonal environmental conditions, since these conditions occur only in temperate zone species of *Ulmus*, *Celtis*, *Zelkova*, and *Hemiptelea*. *Planera aquatica* can be either ring or diffuse porous. *Planera*, when ring porous, has smaller pores in the early wood than do other ring porous ulmaceous genera; and differs from these genera also in the occurrence of spirals in all vessel elements. The less pronounced ring porosity is probably related to the less marked seasonal nature of the environment of *Planera aquatica* in the southeastern United States. Investigations of porosity in several species of *Quercus* from temperate and tropical regions tend to support this conclusion. Scalariform perforations are reported for the first time in the secondary xylem of species of *Celtis*, *Hemiptelea*, *Zelkova*, *Planera*, and *Ulmus*.

ACKNOWLEDGEMENTS

My sincerest thanks and appreciation to Dr. William L. Stern whose guidance, patience, encouragement, and constructive criticism made this study possible. I am grateful to the directors and curators of collections at the Smithsonian Institution, Yale University, and Harvard University for dried wood specimens and to the curators of the United States National Herbarium for dried leaf material. My special thanks to Dr. Richard Howard, Dr. Donald Wyman, and Mr. Henry Goodell of the Arnold Arboretum for their generous help in obtaining living specimens from their collections. I would also like to acknowledge the cooperation of Dr. A. J. Sharp in providing me with dried material of *Mirandaceltis*. For his translations from the Russian language, I gratefully thank Mr. Donald Bissing. My sincere appreciation to Dr. Oswald Tippo for suggesting this problem and for providing me with his slides of elm wood.

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TABLE 1. Genera of Ulmaceae [a]

	Leaf			Flowers			Fruit	
	Habit	Arrangement	Margin					
GENUS	Tree-T Shrub-S	Alternate-A Opposite-O	Entire-E Serrate-S	Bisexual-B Unisexual-U	Sepals, number	Stamens, number	Samara-S Drupe-D Drupe-like-DL Nutlet with wing-N	Geographical distribution
Tribe ULMEAE								
Chaetoptelea Liebm.	T	A	S	B	5	5	S	Mexico to Panama
Holoptelea Planch.	T	A	E	B	4–8	4–8	S	Asia, Africa
Phyllostylon Capanema ex Benth. & Hook. f.	T	A	S	B	5–8	5–8	S	West Indies to Brazil and Argentina
Planera J. F. Gmel.	T	A	S	B	4–5	4–5	S	Southeastern United States
Ulmus L.	T	A	S	B	4–8	4–8	S	Northern Hemisphere
Tribe CELTEAE								
Ampelocera Klotzsch	T	A	E	B,U	4–5	4–10	D	Tropical America, West Indies
Aphananthe Planch.	T,S	A	S	U	4–5	4–5	D	Eastern Asia, Malaya, Australia, Madagascar
Celtis L.	T,S	A	E–S	B	4–5	4–5	D	Temperate and tropical regions
Chaetachme Planch.	S	A	E	U	5	5	D	Southern Africa, Madagascar

Gironniera Gaudich.	T,S	A	E–S	B	5	5	D	Ceylon, Malaya, southern China, Pacific islands
Hemiptelea Planch.	T	A	S	B	4–5	4	N	China
Lozanella Greenman	T	O	S	B	5	5	D	Mexico to Peru
Mirandaceltis Sharp	T,S	A	S	U	5	5	D	Mexico, Central America
Parasponia Miq.	T,S	A	S	B	5	5	D	Malaya, New Guinea Pacific islands
Plagioceltis Mildbr. ex Baehni	S	A	A	B	4	4–5	D	Peru (Willis, 1966)
Pteroceltis Maxim.	T,S	A	S	U	5	5	DL	Northeast Asia
Trema Lour.	T,S	A	S	U,B	4–5	4–5	D	Tropical and subtropical regions
Zelkova Spach	T	A	S	U	4–5	4–5	DL	Eastern Mediterranean to China and Japan

[a] See references to TABLE 1 on p. 523, 524.

TABLE 4a. Dried wood specimens of Ulmaceae examined [a]

SPECIES	COLLECTOR	HERBARIUM VOUCHER [b]	WOOD COLLECTION [c]	ORIGIN
AMPELOCERA				
cubensis Griseb.	Bucher 89	Y[d]	Yw16260[e]	Cuba
edentula Kuhlm.		HB	Yw38271	Brazil
edentula		K	USw26186	British Guiana

TABLE 4a. Dried wood specimens of Ulmaceae examined (*continued*)

SPECIES	COLLECTOR	HERBARIUM VOUCHER [b]	WOOD COLLECTION [c]	ORIGIN
glabra Kuhlm.	Milanez *s.n.*		Yw33906	Brazil
hottlei Standl.	Dugand 665	Y	Yw28486	Colombia
APHANANTHE				
aspera Planch.			Yw9313	Japan
philippinensis Planch.			Yw12326	Philippines
CELTIS				
adolphi-friderici Engl.	Vigne 2595	FHO	Yw23576	Gold Coast
asperifolia Merr.			Yw5619	Philippines
australis L.	Chudnoff 52	HUJ	USw22445	Israel
bungeana Blume	Merrill *s.n.*	Fan Mem. Inst.	Yw19955	China
cinnamomea Lindl.	Van de Koppel 5452	Y	Yw22904	Java
crenato-serrata Merr.			Yw2485	Philippines
harperi Horne	A. C. Smith 4637	Y	Yw28285	Fiji
iguanaea (Jacq.) Sarg.			Yw16698	Panama
iguanaea	Stern, Chambers, Dwyer & Ebinger 550	US	Yw54817	Panama
koraiensis Nakai		Fan Mem. Inst.	Yw23015	China
kraussiana Bernh.			Yw1301	Kenya
laevigata Willd.	Oaks, Nogle & Wilson *s.n.*	F	USw22554	Mexico
laevigata	Wiggins & Rollins *s.n.*	DS	USw34190	Mexico

laevigata (as *C. mississippiensis* Bosc)			Aw3217	United States
latifolia Planch.		L	USw23983	New Guinea
lindheimeri Englm.	Nogle *s.n.*		Yw40672	Texas
luzonica Warb.		CLP	USw32756	Philippines
occidentalis L.		MAD	USw18497	Indiana
pacifica Planch.	MacDaniels *s.n.*	CU	Yw25497	Tahiti
pallida Torr.	Detwiler 90	Y	Yw14815	Arizona
paniculata (Endl.) Planch.	St. John 3679	BISH	Yw37320	Hawaii
paniculata var. *multiseriata* R. Br.	Stokes 445	BISH	Yw24294	Austral Islands
philippinensis Blanco		CLP	USw32730	Philippines
reticulata Torr.			Aw3218J	United States
reticulata		F	USw20024	Texas
rigescens Planch.		L	USw24176	New Guinea
ritensis Planch.		BISH	Yw25895	Fiji
schippii Standl.	Kinlock *s.n.*	Y	Yw40282	British Honduras
schippii	Kinlock *s.n.*	Y	Yw40283	British Honduras
sinensis Pers.	Thomson *s.n.*	F	USw20080	Korea
soyauxii Engl.	Vigne 1208	Y	Yw12670	Gold Coast
swartzii Planch.	Ramoncillo 26	Y	Yw9183	Cuba
tala Gill			Yw6212	Argentina
tenuifolia Nutt.	Keth *s.n.*	MAD	USw22919	Virginia
trinervia Lam.	Scarff *s.n.*		Yw32212	Dominican Republic
ugandensis Rendle			Yw13387	Kenya
wightii Planch.			Yw31688	Java
yunnanensis Schneid.	Ying Pe Chang 36	National Central Univ.	Yw48328	China
zenkeri Engl.			Yw47350	Belgian Congo

TABLE 4a. **Dried wood specimens of Ulmaceae examined** (*continued*)

SPECIES	COLLECTOR	HERBARIUM VOUCHER [b]	WOOD COLLECTION [c]	ORIGIN
CHAETOPTELEA				
mexicana Liebm.	Stern & Chambers 58	Y	USw15582	Panama
mexicana [as *Ulmus mexicana* (Liebm.) Planch.]	Skutch 2040	A	Aw22885	Guatemala
CHAETACHME				
aristata Planch.	Schlieben *s.n.*	B	Yw29375	Africa
microcarpa Warb.			Yw1303	Kenya
GIRONNIERA				
celtidifolia Gaudich.	Waterhouse 149	NY	Yw22860	Melanesia
celtidifolia	A. C. Smith 486	NY	Yw27697	Fiji
cuspidata Kurz			Yw12357	Dutch East Indies
cuspidata	Janssonius 783		Yw31701	Java
nervosa Planch.			Yw12358	Dutch East Indies
nervosa			Yw12359	Dutch East Indies
nitida Benth.			Yw14368	New Caledonia
nitida			Yw13970	New Guinea
subaequalis Planch.		L	Yw20148	New Guinea
HEMIPTELEA				
davidii (Hance) Planch.	Hess *s.n.*	A	Yw35292	Arkansas
HOLOPTELEA				
grandis Mildbr.	Vigne 2504	FHO	Yw23262	Gold Coast

grandis	Donis *s.n.*	BR	USw24390	Congo
integrifolia Planch.		MAD	Yw46153	India
LOZANELLA				
enantiophylla (Donn.-Sm.) Killip & Morton	Stern & Chambers 96	MO	USw16580	Panama
MIRANDACELTIS				
monoica (Hemsl.) Sharp	Sharp 681229	MARY		Mexico
PARASPONIA				
parviflora Miq.	Janssonius *s.n.*		Yw31699	Java
PHYLLOSTYLON				
brasiliensis Cap.	Dugand *s.n.*	Y	Yw23909	Colombia
PLANERA				
aquatica J. F. Gmel.			Yw6699	Florida
aquatica			Yw11169	Florida
aquatica	Wilson *s.n.*	FLAS	USw21789	Florida
PTEROCELTIS				
tatarinowii Maxim.	Ching Wan *s.n.*	Honan Univ.	Yw32019	China
tatarinowii	Ching Wan *s.n.*	Honan Univ.	Yw32143	China
TREMA				
amboinensis Blume	Bryan 2409	BISH	Yw26246	Malaya
angustifolia Planch.	Rahmat Si Boeeca *s.n.*	MICH	USw27851	Sumatra

TABLE 4a. **Dried wood specimens of Ulmaceae examined** (*continued*)

SPECIES	COLLECTOR	HERBARIUM VOUCHER [b]	WOOD COLLECTION [c]	ORIGIN
bracteolata Blume			Yw3958	Africa
guinensis Priemer	Vigne 1206	MAD	Yw12668	Gold Coast
integerrima (Buer.) Standl.	Acosta-Solís 11986	F	USw20464	Ecuador
lamarckiana (Roem. & Schult.) Blume	Stern & Chambers 227	Y	Yw49407	Florida Keys
micrantha (L.) Blume	Stern 118	Y	Yw49444	Florida Keys
orientalis (L.) Blume		CLP	USw32599	Philippines
vieillardii (Planch.) Benth. & Hook.			Yw13988	New Caledonia
virgata Blume	Tang 215	Fan Mem. Inst.	Yw21827	China
ULMUS				
alata Michx.		A	Aw9054	United States
alata		A	Aw3220	United States
alata		F	Yw26935	Missouri
americana L.		A	Aw3215	United States
americana		MAD	USw18087	Indiana
canescens Melville	Chudnoff 62	HUJ	USw22478	Israel
crassifolia Nutt.		A	Aw3221	United States
glabra Huds.			Yw21586	United States
glabra		US	Yw53493	United States
glabra (as *U. campestris* L.)			Aw9063	Europe
glabra (as *U. campestris*)			Aw9064	Europe
glabra (as *U. campestris*)		FHO	Yw19691	England

hollandica Duroi		FHO	Yw36401	England
hollandica	Clevenger 1274	CLM	USw20605	Ohio
laciniata (Trautv.) Mayr		A	Aw9662	Japan
laciniata		TOFO	USw23712	Japan
laevis Pall.		LE	USw30703	U.S.S.R.
macrocarpa Hance		Fan Mem. Inst.	Yw23012	China
major J. E. Smith		FHO	Yw21587	England
major		FHO	Yw19685	England
minor Mill.		FHO	Yw19687	England
montana With.	Jack 201	A	Aw9078	United States
montana		A	Yw9079	England
montana		FHO	Yw19686	England
nitens Moench		FHO	Yw19689	England
parvifolia Jacq.	Kanehira 92	FHO	Yw6493	Formosa
plotii Druce		FHO	Yw50005	England
procera Salisb.	Clevenger 1272	CLM	USw20603	Ohio
procera	Clevenger 1261	CLM	USw20604	Ohio
pumila L.	Hicock *s.n.*	A	Yw40235	Connecticut
rubra Muhl. (as *U. fulva* Michx.)		A	Aw9069	United States
rubra (as *U. fulva*)		A	Aw3214	United States
scabra Mill.		DOZ	Yw23180	Poland
serotina Sarg.		A	Aw9082	Illinois
serotina	E. S. Harrar 8474	DUKE	Yw43454	United States
sieboldii Daveau	Pilcher 124		USw21177	Japan
stricta Lindl.		FHO	Yw19690	England
suberosa Ehrh.		DOZ	Yw23154	Poland
thomasii Sarg.	Schmidt *s.n.*	MAD	USw23450	United States
uyematsii Hayata	Fiyioka *s.n.*	TI	Yw24060	Formosa

TABLE 4a. **Dried wood specimens of Ulmaceae examined** (*continued*)

SPECIES	COLLECTOR	HERBARIUM VOUCHER [b]	WOOD COLLECTION [c]	ORIGIN
wallichii Planch.		Pakistan Forest Research Institute	Yw49654	Pakistan
ZELKOVA				
keakii (Sieb.) Maxim.			Yw2003	Japan
serrata (Thunb.) Nakai		TOFO	USw23713	Japan

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[a] See reference to TABLE 4a on p. 532.

[b] Abbreviations follow those recommended by Lanjouw & Stafleu (1964) in *Index Herbariorum*.

[c] Abbreviations follow those recommended by Stern (1967) in *Index Xylariorum*.

[d] Y refers to the herbarium and Yw to the xylarium formerly located at the Yale University School of Forestry, but now housed at the U.S. Forest Products Laboratory, Madison, Wisconsin, as the Samuel James Record Memorial Collection.

TABLE 4b. **Dried leaf specimens of Ulmaceae examined** [a,b]

SPECIES	COLLECTOR	ORIGIN
AMPELOCERA		
cubensis Griseb.	Ekman 9470	Cuba
edentula Kuhlm.	Ducke 1736	Brazil
hottlei Standl.	Ll. Williams 9497	Mexico
APHANANTHE		
aspera Planch.	Chiao 2935	China
philippinensis Planch.	Edaño 26773	Luzon
CELTIS		
bungeana Blume	Wilson 10459	Korea
caudata Hance	Callado 9592	Mexico
iguanaea (Jacq.) Sarg.	Standley 1500	Mexico
laevigata Willd.	Thieret 16497	Louisiana
laevigata var. *texana* (Scheele) Sarg.	Lodewyks 382a	Missouri
occidentalis L.	Allard 7931	Virginia
occidentalis var. *crassifolia* (Lam.) A. Gray	Peck *s.n.*	New York
pallida Torr.	Killip 32729	Arizona
philippinensis Blanco	Conteras 23396	Philippines
pubescens Granat.	Pickel 1177	Brazil
pumila Pursh	Harbison *s.n.*	Virginia
reticulata Torr.	Johnson 8580	Arizona
reticulata (as *C. douglasii* Planch.)	Jahn 8449	Washington
schippii Standl.	Little 6216	Ecuador
sinensis Pers.	Lau 388	China
spinosa Ruiz	Jorgenson 3853	Paraguay
tenuifolia Nutt.	Fernald & Long 13326	Virginia
tenuifolia	Terrell & Barclay 3373	Alabama
triflora Lam.	Smith & Klein 11162	Brazil
trinervia Lam.	Webster 3679	Cuba
CHAETACHME		
aristata Planch.	Zenker & Haudz 430	French Cameroons
microcarpa Rendle	Piemeisel & Kephart 21	Kenya
CHAETOPTELEA		
mexicana Liebm.	Standley 20002	Mexico
GIRONNIERA		
celtidifolia Gaudich.	Beer 7082	Solomon Islands
cuspidata Kurz	Lei 831	China
nervosa Planch.	Low & Motan 94530	Malay Peninsula

TABLE 4b. **Dried leaf specimens of Ulmaceae examined**[a,b] (*continued*)

SPECIES	COLLECTOR	ORIGIN
nitida Benth.	Taan 1629	Hong Kong
parvifolia Planch.	King 5369	Malay Peninsula
reticulata Thw.	Piolane 10768	South Vietnam
HEMIPTELEA		
davidii (Hance) Planch.	Dorsett 564	China
HOLOPTELEA		
integrifolia Planch.	Choudhury 108	India
LOZANELLA		
enantiophylla (Donn.-Sm.) Killip & Morton	Hinton 14286	Mexico
MIRANDACELTIS		
monoica (Hemsl.) Sharp	Andrle 51	Mexico
monoica	Andrle 103	Mexico
PARASPONIA		
andersonii Miq.	Baumann 6138	New Caledonia
PHYLLOSTYLON		
brasiliensis Cap.	Kuhlmann 17991	Brazil
rhamnoides Taub.	Dugand 5511	Colombia
PLANERA		
aquatica J. F. Gmel.	Palmer 15124	Florida
PTEROCELTIS		
tatarinowii Maxim.	Chiao 3085	China
TREMA		
amboinensis Blume	Santos 4656	Philippines
canescens Blume	Garnier 688	Nicaragua
lamarckiana (Beur.) Standl.	Small 8078	Florida
micrantha (L.) Blume	Dressler 1660	Mexico
orientalis (L.) Blume	Henry 12189A	China
ULMUS		
alata Michx.	Moore & Horton 6740	Louisiana
americana L.	Hoy 521	New York
carpinifolia Gleditsch	Harrison 10593	Utah
crassifolia Nutt.	Palmer 24050	Oklahoma
glabra Huds.	Norman *s.n.*	Spain
glabra (as *U. campestris* L.)	Baenitz *s.n.*	Poland
hollandica Duroi	Sonnobree 3523	Belgium

TABLE 4b. **Dried leaf specimens of Ulmaceae examined**[a,b] *(continued)*

SPECIES	COLLECTOR	ORIGIN
laevis Pall.	US1750849	Poland
minor Mill.	David 3A	England
montana With.	Paulsen *s.n.*	Denmark
parvifolia Jacq.	Howell 26645	California
parvifolia	Terakawa 136	Japan
pumila L.	Purdon 1048	China
rubra Muhl. (as *U. fulva* Michx.)	Humphrey *s.n.*	Wisconsin
rubra (as *U. fulva*)	Sheldon *s.n.*	Minnesota
serotina Sarg.	Biltmore Herb. 3634	Georgia
thomasii Sarg.	Toumey *s.n.*	Connecticut
ZELKOVA		
carpinifolia (Pall.) Koch	Sudworth *s.n.*	District of Columbia
serrata Makino	Sudworth *s.n.*	District of Columbia
sinica Schneid.	Pei 3077	China

[a] All dried leaf specimens obtained from United States National Herbarium, Smithsonian Institution, Washington, D.C.

[b] See reference to TABLE 4b on p. 532.

TABLE 4C. **Preserved leaf and wood specimens of Ulmaceae examined** [a,b]

SPECIES	HERBARIUM VOUCHER	RANGE [c]
CELTIS		
bungeana Blume	A643–53	Central and northern China, Manchuria, and Korea
jessoensis Koidz.	A7532	Korea and Japan
laevigata Willd.	A112–54–A	Southern Indiana and Illinois to Texas and Florida
laevigata var. *smallii* (Beadle) Sarg.	A1165	North Carolina and Tennessee to Georgia and Alabama
occidentalis L.	A36937B	Quebec to Manitoba, south to North Carolina, Alabama, and Kansas
occidentalis var. *cordata* Pers.	A15954A	United States
pumila Pursh	A12999B	New Jersey to Florida, west to Kansas, Colorado, and Utah
reticulata Torr.	A587–56A	Colorado and Texas to Washington and southern California
reticulata (as *C. douglasii* Planch.)	A21779	Colorado and Texas to Washington and southern California
tournefortii Lam.	A593–56B	Mediterranean region
HEMIPTELEA		
davidii (Hance) Planch.	A5283	Northern China, Manchuria, and Korea
TREMA		
lamarckiana (Roem. & Schult.) Blume	MARY, Stern 2660	Florida Keys and southern Florida
micrantha (L.) Blume	MARY, Stern 2661	Florida Keys and southern Florida
ULMUS		
americana L.	MARY, Sweitzer, *s.n.*	Newfoundland to Florida and west to Rocky Mountains
carpinifolia Gleditsch	A17883	Europe, northern Africa, and western Asia
carpinifolia var. *suberosa* (Moench) Rehd.	A17880	Europe
glabra Huds.	A17143	Northern and central Europe, western Asia

hollandica Mill.	A17921	Europe
laevis Pall.	A17910	Europe, western Asia
procera Salisb.	A90–4–38	England, western and southern Europe
pumila L.	A15936	Eastern Siberia, northern China, and Turkestan
pumila var. *arborea* Litv.	A15939	Turkestan
rubra Michx.	A21966A	Eastern United States, west to Texas, Oklahoma, Nebraska, North Dakota, and north to Quebec
thomasii Sarg.	A17925F	Quebec to Tennessee, west to Nebraska

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[a] All specimens were collected at the Arnold Arboretum, Boston, Massachusetts, except those with MARY herbarium vouchers, where the collector's name is listed.

[b] See reference to TABLE 4c on p. 532.

[c] Ranges were taken from Planchon (1873), Rehder (1940), L. H. Bailey (1949), and Little (1953).

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THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 16. THE FLOWERING CYCLE AND AN INTERPRETATION OF ITS SEASONALITY

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THIS STUDY WAS UNDERTAKEN as a part of the investigation of the dynamics of a forest located on Pico del Oeste, in the Sierra de Luquillo of Puerto Rico.[1] Pico del Oeste is the third highest peak (1050 meters) of the Luquillo formation and is located slightly northwest of Pico del Este. The summit is covered by a dense stand of trees and shrubs of small stature which form a peculiar vegetation type known as the elfin forest. The plants are evergreen and usually festooned with flowering and non-flowering epiphytes. While preceding papers in this series have stressed the multi-faceted peculiarities of the elfin forest, this paper is intended to stress one aspect which the elfin forest has in common with all other forests — the reproductive cycle.

There are few organized records of flowering times for tropical plant species and those which exist have been in large part compiled by monographers or floristic workers, largely on the basis of herbarium specimens. The elfin forest study seemed therefore to be a unique opportunity to obtain reliable flowering and fruiting data. These data, particularly the resulting patterns of flowering and fruiting, have been useful in helping to focus attention on a number of questions such as an interpretation of seasonality, responses to seasonality, comparative studies with lowland floras, and the relative roles of vegetative and sexual reproduction. Only after some of these questions were explored was it possible to consider properly the origin of the floristic elements of the Pico del Oeste elfin forest. The "flora" is a small one and was found to consist of 15 species of Monocotyledons and 40 species of Dicotyledons plus the non-flowering species (see Howard, 1968; Fulford *et al.*, 1970; and Foerster 1971 for details of the latter). According to Howard (1968) approximately 14 percent of the monocots and 55 percent of the dicots are endemic to Puerto Rico. A general endemism for the plants of the Sierra de Luquillo has been suggested as about 18 percent. Although the species of Pico del Oeste show a high percentage of endemism (i.e., they are restricted to Puerto Rico) I do not believe any species is restricted solely to the elfin forest formation. A general statement that the species components of this elfin forest also occur as a part of the flora at somewhat lower altitudes seems pertinent. The Pico flora may be considered as derived from a portion of the flora found at lower elevations; the reason for the small number of flowering species being that few of the species are adapted to the prevailing climatic conditions of the elfin forest.

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[1] This study was partially supported by a grant from the National Science Foundation (GB-3975) to Dr. R. A. Howard, principal investigator.

FLOWERING

Preliminary transects of the site were made in the fall of 1965 when tentative identifications were obtained from representative collections. These determinations formed the basis of a checklist of the plants of Pico del Oeste and representative specimens were labelled both at canopy and ground level (for details see Howard, 1968). This labelling proved to be of particular importance because of the number and variety of personnel who were to be involved in the maintenance of the records. The "flora" could be learned in a relatively short period and the number of misidentifications was kept to a minimum. Weekly records of flowering and fruiting were kept from February 1966 to January 1968 inclusive, and the completeness of the record attests to the faithfulness of all persons concerned.

The weekly flowering and fruiting records were combined into a single cumulative monthly record which is presented in TABLE 1. The records are restricted to the plants growing on the site and do not include individuals of the same species growing at lower altitudes or in other geographic localities. The scoring was on the basis of all or none. Quantity was not scored inasmuch as few individual observers had previous experience with the species under study and had no point of reference in this regard.

There are a few abnormalities in the record which lead me to the conclusion that the two-year record, while useful, does not give an accurate indication of the sexual reproductive cycles of the plants of Pico del Oeste. Extended observations would tend to show more variability than is now shown for some of the species. The flowering record must be considered to be more accurate than that for fruiting as most observers had the tendency to begin scoring a plant in fruit as soon as fruit development became apparent. In many instances, however, mature fruit did not develop during the course of the observations. There are a few additional anomalies in the flowering record which must be commented upon. The record for *Andropogon bicornis* is incomplete as it was represented by a single clump which was destroyed accidentally very early in the study period. *Arthrostylidium sarmentosum* is known in flower only from one previous collection, and because of its very reduced inflorescence may have been overlooked if and when it did flower. *Rajania cordata* failed to flower on the study site, although it flowers conspicuously at lower altitudes. *Trichilia pallida* and *Hillia parasitica* were represented by juvenile plants only and may not be regular members of the community. *Renealmia antillarum* and *Lobelia portoricensis* were each represented by a single large specimen but as they both flowered continuously no record gap exists. In one species, *Vriesea sintenisii*, the flowering record as given in TABLE 1 may be exaggerated. This *Vriesea* is few-flowered and the white flowers last for a few days only. In contrast the inflorescences are long-persistent

Table 1. **Cumulative monthly flowering and fruiting records for Pico del Oeste**[1]

Family and Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Gramineae												
Andropogon bicornis		+*										
Arthrostylidium sarmentosum												
Ichnanthus pallens	+*	+*	+*	+*	+*	+*	+*		*			*
Isachne angustifolia		+*	+*	+*	+*	+*	+*	+*	*	*		+*
Cyperaceae												
Carex polystachya	*		+*	+*	+*	+*	+*	+*	+*	*	*	*
Eleocharis yunquensis	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
Scleria secans	+*	*	+*	+*	+*	+*	+*	+*	+*	*	+*	
Palmae												
Prestoea montana	+*	+*	*	*	*	+*	+*	+*	+*	+*	+*	*
Araceae												
Anthurium dominicense	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
Bromeliaceae												
Guzmania berteroniana	*		*	*		+	+*	+*	+*		+	+*
Vriesea sintenisii	*	+*	*	+*	+*	+*	+*	+*	+*	+*	+*	*
Dioscoreaceae												
Rajania cordata												
Zingiberaceae												
Renealmia antillarum	+*	+	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
Orchidaceae												
Brachionidium ciliolatum[2]	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	*
Dilomilis montana	+	+*	+*	+*	+*	*	+					+*

Piperaceae												
Peperomia emarginella						+	+	+	+*	+*	+*	
Peperomia hernandiifolia	+*	+*	+*		+*	+*	+	+*	+*	+*	+*	+*
Chloranthaceae												
Hedyosmum arborescens	+	+	+*	+*	+	+*	+*	*	+*	+		
Moraceae												
Cecropia peltata	+			+	+*	+*	*				+	+
Urticaceae												
Pilea krugii			+*	+*	+*	+*	+*	+*	+*	+*	+*	
Pilea yunquensis		+	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
Lauraceae												
Ocotea spathulata	*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
Meliaceae												
Trichilia pallida												
Aquifoliaceae												
Ilex sintenisii	*			+	+*	+*	+*	+*	+*	+*	+*	+*
Celastraceae												
Torralbasia cuneifolia							+		+		+	
Ochnaceae												
Sauvagesia erecta	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
Marcgraviaceae												
Marcgravia sintenisii	+*	*	*	+*	*	+*	+*	+	+*	+*	+*	+*
Theaceae												
Cleyera albopunctata	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*

TABLE 1. **Cumulative monthly flowering and fruiting records for Pico del Oeste** (*continued*)

FAMILY and SPECIES	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
GUTTIFERAE												
Clusia grisebachiana			*				+*			+		
BEGONIACEAE												
Begonia decandra	+		+*	+	+	+	+*	+*	+	+	+*	+
MYRTACEAE												
Calyptranthes krugii	*	*			+	+	+	+	+*	+*	+*	*
Eugenia borinquensis	+*					+	+	+*	+*	+*	+*	+*
MELASTOMATACEAE												
Calycogonium squamulosum							+			+	+	+
Mecranium amygdalinum	+						+	+			+*	+*
Miconia foveolata	+*	+	+*	+*	+*	+*	+*	+*	+*	+*	*	+*
Miconia pachyphylla	+	+	+*	+*	+*	+*	+*	*	*	+*	*	
Miconia sintenisii	+	+*	+*	*	*				+*	+*		+
ERICACEAE												
Gonocalyx portoricensis	+	+	+*	+*	+*	+*	+*	+*	+*	+	+	+*
Hornemannia racemosa		+	+	+*		+*	+*	+*	+*	+	+*	
MYRSINACEAE												
Ardisia luquillensis	+*	+*	*	+*	*	*	+*	*	+	+*	+*	+*
Cymbianthopsis sintenisii [3]	*					+	+	+	+*	+*	+*	+*
Wallenia yunquensis	*	*	+*	+*	+*	+*	+*	+	+*	+*	+*	+*
SAPOTACEAE												
Micropholis garciniifolia	+*		+			+	+*	+*	+*	+*	*	

SYMPLOCACEAE												
Symplocos micrantha	+		+				+					
OLEACEAE												
Haenianthus salicifolius	+*									+*	+*	
CONVOLVULACEAE												
Ipomoea repanda	+*									+	+	+
BIGNONIACEAE												
Tabebuia rigida	+	+	+	+	+	+	+	+	+	+	+	+
GESNERIACEAE												
Alloplectus ambiguus	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
Gesneria sintenisii	+*	*	+*							+	+*	+*
ACANTHACEAE												
Justicia martinsoniana	+*	+*	+*	+*	+*	+*	+*	+		+	+	+*
RUBIACEAE												
Hillia parasitica												
Psychotria berteriana	+*	+	+*	+*	+*	+*	+*	*	*	+	+	+
Psychotria guadalupensis	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
CAMPANULACEAE												
Lobelia portoricensis	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
COMPOSITAE												
Mikania pachyphylla		+	+*	+*	+*	+*	+*					

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[1] Plus sign (+) = flowering; asterisk (*) = fruiting.

[2] *Brachionidium ciliolatum* Garay (Jour. Arnold Arb. **50**: 464. 1969) has been treated as *B. parvum* Cogn. in previous papers in this series.

[3] *Cymbianthopsis sintenisii* (Urb.) Lundell (Wrightia **4**: 68. 1968) has been treated as *Grammadenia sintenisii* (Urb.) Mez in previous papers in this series.